Systematic Zoology

Museum
QL
1
.5997
v.4
no.3

SOCIETY OF SYSTEMATIC ZOOLOGY

Museum Library

Symposium: Animal Courtship Patterns

Mating Activities of Balloon Flies — *E. L. Kessel* — 97

Courtship and Mating in Salientia — *D. L. Jameson* — 105

Systematic Study of Anthozoan Nematocysts — *C. E. Cutress* — 120

Brown; Savory: Scientific Terminology — *O. Haas* — 138

Points of View — *Fennah; Sabrosky; Hyman; Cain* — 140

VOLUME 4 SEPTEMBER 1955 NUMBER 3

UNIVERSITY OF MICHIGAN LIBRARIES

UNIVERSITY OF MICHIGAN LIBRARIES

Systematic Zoology

JOHN L. BROOKS, *Editor*

Editorial Board

P. J. DARLINGTON, JR. — G. E. PICKFORD
L. R. DICE — C. W. SABROSKY
E. MAYR — G. W. SINCLAIR

SYSTEMATIC ZOOLOGY is published quarterly, on or about the tenth day of March, June, September, and December, by the Society of Systematic Zoology. Manuscripts and correspondence about the contents of the journal and other editorial matters should be addressed to the editor, Dr. John L. Brooks, Osborn Zoological Laboratory, Yale University, New Haven, Conn.

Subscription rates are $4.00 to members, $7.00 to non-members and institutions. The price of single numbers, when available, is $1.50 to members and $2.00 to non-members. Annual dues are $1.00. Correspondence regarding subscriptions, membership, purchases, non-receipt, and other non-editorial business should be addressed to the secretary-treasurer of the Society, Dr. R. E. Blackwelder, Room 429, U. S. National Museum, Washington 25, D. C.

The Society of Systematic Zoology

OFFICERS FOR 1955

President.....L. M. KLAUBER
San Diego Soc. Natural History

President-Elect.....G. W. WHARTON
University of Maryland

Secretary-Treasurer.....R. E. BLACKWELDER
U. S. National Museum

THE COUNCIL

D. F. HOFFMEISTER	1955	H. W. MANTER
J. S. ROGERS	1956	H. M. SMITH
C. W. SABROSKY	1957	F. A. URQUHART
R. H. ARNETT, JR.	1958	W. I. FOLLETT

Entered as second-class matter at the post office at Washington, D. C., with an additional entry at Baltimore, Maryland.

Animal Courtship Patterns

THIS SYMPOSIUM was held at the annual meeting of the Society of Systematic Zoology on December 7, 1954, at Berkeley, California.

Participants

EDWARD L. KESSEL • *The Mating Activities of Balloon Flies*

DAVID L. JAMESON • *Evolutionary Trends in the Courtship and Mating Behavior of Salientia*

UNIVERSITY OF MICHIGAN LIBRARIES

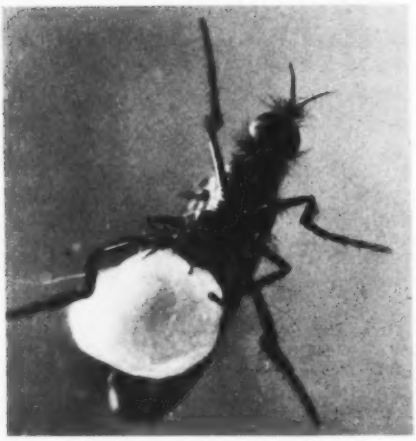

FIG. 1. Male of *Empimorpha geneatis* carrying balloon.

FIG. 2. Front end of balloon of *Empis bullifera* showing attached prey. Note that prey is large relative to balloon and still edible by female (Stage 5).

FIG. 3. Balloon of *Empimorpha geneatis* dropped on the tip of a pine needle. Note that the inedible body of the prey is small relative to the balloon. The protruding head and thorax are used as a handle by the male (Stage 7).

The Mating Activities of Balloon Flies

EDWARD L. KESSEL

IN 1875, while visiting in the Swiss Alps, Baron Osten-Sacken made the first recorded observations on what we now call balloon flies. On sunny days, between the hours of about 9 and 10 o'clock, he noticed brilliant, silvery flashes among the sunbeams which penetrated the shadows of the fir forest. When he concentrated his attention on the flashes he concluded that they must be produced by insects, so he determined to catch some and added an extension to his net handle. The white flashing objects seemed to dodge with agility and it was only after several swings that he was certain he had netted one of them. However, when he looked into the net, he was at first astonished to see only an inconspicuous dull-colored fly, much smaller than he had anticipated. He assumed that this one had been captured by accident, along with the one he had tried for. So he examined his net carefully and it was only then that he noticed the white, filmlike packet of sparkling material on the gauze. He tried to pick it up, but it was so light that his breath carried it away. He pursued it and finally eased it into a vial. This was the first of the so-called fly-balloons to be taken.

To make certain that the balloons actually were associated with the flies, Osten-Sacken caught one specimen after another, always with the same results. Each time there was the balloon in the net along with the fly. And examining the flies with his hand lens, he observed that invariably they were males. (See Fig. 1.)

It was Becker (1888) who described this fly that Osten-Sacken had discovered, and he named it *Hilara sartor*. *Hilara* is a genus of the family Empididae which is made up of the dance flies, so called because of the habit indulged in by many species of dancing on the wing in assemblages which sometimes reach huge proportions. All of the balloon-making flies belong to the Empididae.

Becker was interested in natural history as well as taxonomy, so he joined Osten-Sacken in speculation as to what the significance of the balloon might be. In fact he went to observe the flies in their home environment, but they flew too high for him to get close enough to make accurate observations. As a result he reached the erroneous conclusion that the males carry the white structures on their backs. He also supposed that these structures serve as decorations which attract the attention of the females, and of course in this he was not far wrong.

That same year Mik (1888) also went to see these flies in action, and apparently he had either better eyesight or a taller stepladder than Becker because he was correct in insisting that the flies carry the balloons below their bodies, where they are suspended by the legs. He observed, moreover, that these structures are considerably flattened, this flattening being much more pronounced than in any of the later-discovered species. This observation led him to propose the fantastic theory that the male hilaras use the flattened objects as aeronautical surfboards on which to cavort among the sunbeams.

The next entomologist to speculate on the significance of the balloons was Verhoff (1894). He concluded that they must serve as warning signals to birds and predaceous insects. There is no evidence that these flies are distasteful to birds; on the contrary I have seen birds attack swarms of related species of empidids. In regard to the second part of Verhoff's

UNIVERSITY OF MICHIGAN LIBRARIES

contention, namely, that their scintillating balloons serve to protect them from predaceous insects, this is nearer the truth, although not in the sense that Verhoff had in mind. The predaceous insects in this case are not other forms as one might suppose, but rather the females of the male's own species. Empidid flies are generally predaceous, this being true for the female as well as the male. And the potential empidid bride might be more hungry than amorous, at least in the early stages of courtship. We now know that the balloons serve three functions: (1) to provide a "come hither" invitation to the female instead of a warning; (2) to distract the female from her predaceous inclinations once they have embraced; (3) to serve as a stimulus to mating. What are some of the details of this fascinating story, and how were they discovered?

Evolutionary Stages

The problem presented to the early workers by the case of *H. sartor* was so perplexing because it represents the end stage in a complex evolutionary sequence. But as more and more species of these balloon-making flies were discovered, the significance of the light-reflecting structures which they carry in their aerial dances became apparent. Hamm (1928) suggested three more or less distinct stages, and Melander (1940) added a fourth. While I find it necessary to disagree with these authors as to the origin of the material from which the balloon is made, I nevertheless accept the four general stages which they have suggested. However, during the eight years that I have been making observations on balloon flies, I have attempted to analyze still further the details of this evolutionary sequence and have come to recognize eight stages in all. These are as follows:

Stage 1: The first stage is simply that of a predaceous species in which the male does not bear a wedding gift for his bride. There are numerous species of empidids, e.g., those of the genus *Tachydromia* which represent this basic stage. The prey is captured and devoured by the sexes independently. This stage differs in no way from the cases of ordinary predaceous species, such as those which occur in other insect families. Sometimes the prey may belong to the same species as the captor, and the female may, on occasion, include the male among her victims.

Stage 2: In the second stage the male avoids any cannibalistic attention on the part of the female by carrying with him, ready for presentation at the moment they embrace, a wedding present in the form of a juicy insect. The male first catches the prey, and then he flies about with it in search of a mate. *Empimorpha comata* and certain species of *Rhamphomyia* and *Empis* represent this stage. Often the prey carried by the bride-hunting male is as large as he is, and on one occasion I captured a male carrying two bibionid flies, each almost as large as himself. This was surprising inasmuch as it would be supposed that the instinctive urge to accomplish the prey-catching step in this mating pattern would be satisfied by the capture of one fly. In this second stage the prey is simply eaten by the female, the gift serving merely to occupy her attention as she passively accepts the male during the time she is thus distracted. The mating lasts as long as the food does.

Stage 3: While the third stage is similar to the second, it differs in two important respects. As in the second, the male first catches the prey, but in this stage he does not go in search of a female. Instead, he joins other males, bearing gifts, in an aerial dance of eligible bachelors. When a female approaches, the males do not take after her, but instead continue to dance in the swarm. The female, on approaching such a swarm, must take the initiative, and it is worth while noting at this point that this is a feature common to all of the remaining stages in the series of mating patterns to be described. In this third stage, the prey has become the stimulus for mating, and it no longer serves merely

as a distraction to save the male's life. The female enters the swarm and selects one of the dancing males, they embrace and she accepts the gift, and the two continue to fly in the swarm. In some species the female feeds on the prey while copulation is under way and the pair are still flying. In other forms the female indicates that her primary interest is in mating, for she abstains from feeding until such time as the two flies leave the swarm and settle on some nearby vegetation. Here she has her meal and copulation again continues as long as the food lasts. Certain species of *Hilara* and *Rhamphomyia* represent this stage.

Stage 4: In the fourth stage the male bears a wedding gift which, as before, consists of a prey, but now something has been added. Pasted haphazardly here and there against the prey are shiny viscid globules or, as in certain cases, the prey is more or less entangled in silken threads. Here we are dealing with a number of species of *Hilara*. In this stage it is still the prey which serves as the mating stimulus for the female, the simple wrappings being unimportant in this regard. These entangling structures help to quiet the newly captured prey and doubtless that is their sole function.

Stage 5: In the fifth stage the simple wrappings of the fourth stage have been elaborated to form the complex structure which we call a balloon, and this structure shares with the relatively large prey the function of stimulating mating. This stage is illustrated by two balloon-making forms of the genus *Empis* which occur in western United States. These are *Empis aerobatica* Melander and *Empis bullifera* Kessel and Kessel. The former was studied by Aldrich and Turley (1899), and my wife and I (Kessel and Kessel, 1951) have published on the latter. Evidently the two species are very closely related; not only are the flies structurally very much alike, but their balloons are also very similar. However, there are a number of discrepancies between the accounts of the observations made on the two species. These differences will be considered in connection with the account of *E. bullifera*, given below.

It was in the spring of 1949 that we discovered the first representatives of the species that was to be known as *E. bullifera*. We named it *"bullifera"* because of its bubble-bearing activities. To date these flies seem not to have been seen anywhere except on our home property (five acres of woods at Novato, in Marin County, California, about thirty miles north of San Francisco). They have recurred there every year since they were discovered. These flies have been observed mostly as mating pairs, drifting in lazy flight, first in one direction and then in another, back and forth within the clearing under the trees, their glistening white balloons producing flashes whenever they penetrate a sunbeam. Sometimes the flight becomes so slow that the balloon appears to hang almost motionless in one spot. Then, without warning, the flies will make one to several quick turns, sometimes to leave the clearing altogether, but more often to resume their casual flight nearby. Always they can be followed easily by the conspicuous balloon which they carry.

If one looks at the balloon with the naked eye, it appears to be made up of fine, shiny, white fibers which are wound spirally into a thin-walled, hollow sphere. Covering the front of the balloon (front in the sense that the fly normally carries the balloon with this end forward) and somewhat entangled in its threads and globules is the prey. We have found the prey of this species to consist of midges, psocids, or tiny spiders. In this fifth stage of the evolution of the balloon-making habit the prey is still large in comparison with the size of the balloon and it is still fed on by the female (Fig. 2).

The balloon of this species is open behind, and when viewed from this point it resembles a tiny, filmy, white vespid nest. If one focuses down through the opening into the cavity of the balloon one can often see the tangled legs of the prey within.

UNIVERSITY OF MICHIGAN LIBRARIES

Highly magnified, the balloons show numerous irregularities; the spirals which compose the walls are in some places piled two or three deep, while in a few places open spaces have been left. Most of the apparent fibers of the balloon are seen actually to be beadlike chains of tiny bubbles, although adhering haphazardly to the surface of the balloon one frequently finds silklike threads which must be the result of the drawing out of the balloon-forming material before it has hardened. We have sometimes observed similar silken threads adhering to the tips of the abdomens of male balloon flies, indicating that the threads, as well as the globules of the balloons, originate from this source. As for the bubbles of the balloon, these tiny spheres are thin-walled, white, transparent, and iridescent, and look like miniature soap bubbles. They are about equal in size and are clearly arranged to form a distinct chain which is spirally wound to form the hollow balloon, the viscous bubbles of one loop adhering to those of the loop before and the loop after.

Most of our observations have been made on mating pairs of *E. bullifera*, and no swarms of dancing eligible bachelors have yet been discovered for this species. In only one case was an unmated male found with a balloon, and this, judging from its appearance, was under construction; unfortunately the fly did not remain for observation but flew away almost immediately. Although no flies were actually observed making the balloons, I am convinced that the bubbles are formed at the anal aperture and applied to the body of the prey with the tip of the abdomen. The prey, grasped by the legs, is touched by the tip of the underthrust abdomen, and as the first bubble is extruded it adheres to the captured arthropod. Each successive bubble sticks to the preceding one, and the chain formed in this manner is attached in a ring on the prey by a circling motion of the abdomen. As construction continues and the balloon increases in size toward the rear, the curved-under portion of the male's abdomen becomes shorter and shorter and, as the length of this portion decreases, movement of the abdomen's tip becomes more and more difficult. Perhaps this accounts for the balloon's being left open in the rear. It is interesting to note that the balloon of *E. aerobatica*, which was studied by Aldrich and Turley (1899), was likewise open at the rear.

On only one occasion did we observe the second phase of the mating pattern in *E. bullifera*. Remember that in this stage 5, copulation begins in the air when the insects embrace and the balloon is transferred to the female. But, as stated above, she does not feed on the prey during this first phase of mating. One morning a flying pair were observed drifting directly out of the clearing toward an area of low shrubs. Here they settled on a slender stem of snowberry, about one foot above the ground. Here the male, who had been astride the female in flight, grasped the stem and supported the pair while the female held the balloon with her feet. It was then that the female began to probe the prey with her mouthparts, turning the balloon over and over between thrusts of her proboscis. She seemed to be trying to suck the prey's juices from all parts of its body by piercing it at many points and in different directions in a haphazard manner. Sometimes her proboscis probed through the balloon itself to get to the prey and as a result of this and constant manipulation, the balloon became very ragged. When the female had concluded her meal some thirty minutes later, she abruptly dropped the mauled balloon and terminated the mating.

It has been mentioned that there are discrepancies between the observations made by Aldrich and Turley (1899) on *E. aerobatica* and those which my wife and I have made on *E. bullifera*. Yet not only are these two species members of the same genus, but their members are much alike anatomically. Moreover, their balloons are very similar, even to the detail of being open behind. This makes it difficult for

me to accept the assertion of Aldrich and Turley that when the sexes embrace the female takes a position on the male's back and he continues to carry the balloon. In no species of Empididae, and I have examined many mating pairs of several different species, have I found the female astride the male. McAtee (1909) has also observed that the claim of Aldrich and Turley is at variance with his observations. He examined hundreds of mating pairs of *Empis spectabilis,* and although this species is not a balloon-maker, the female was in possession of the prey and the male was the upper member of the pair in every case. Aldrich and Turley seem to have continued to confuse the sexes even after the pair settled on vegetation for the second phase of mating. To quote from their account, "After copulation had begun, the pair would settle down towards the ground, select a quiet spot, and the female would alight by placing her front legs across a horizontal grass blade. . . . Here she would continue to hold the male beneath her. . . . The male, meanwhile, would be rolling the balloon about in a variety of positions, juggling with it, one might almost say." For the male to retain possession of the prey and balloon throughout mating, as these authors state, would rob the whole balloon-making procedure of its significance. It is probable that Aldrich and Turley were misled by their knowledge that the genitalia of male empidids are always upturned and they would therefore presume that the male would have to be below the female in copulation. But our observations show that the abdomens of the two sexes cross, and this crossing places the tip of the male's abdomen in position below that of the female.

Stage 6: In the sixth stage the prey again serves as the stimulus for the male to construct the complex balloon. Now, however, the prey no longer serves as food for the female. It is somewhat smaller than in the preceding stage and it is probable that the male consumes what fluid it contains when he captures it. At any rate it is no longer edible when the sexes embrace and the male passes the balloon to the female. In this stage, however, the prey, still being conspicuous enough to be easily noticed, doubtless continues to share with the balloon the function of stimulating copulation. It is possible that *Empis aerobatica* represents this stage instead of the fifth, but the observations of Aldrich and Turley were too superficial for us to decide. These investigators presumed that the tiny fly pressed into the front of the balloon was for food but they make no mention of having seen either member of the pair feed on it. Although they did confuse the positions of the sexes, there would hardly be an excuse for their failing to see the lower partner feed if indeed it did. If the female did not feed, even after settling on vegetation, then this species would represent this sixth stage.

Stage 7: In stage 7 the prey is yet smaller; in fact it is always minute and so delicate that it would seem to be useless as food even for the male when first captured. The abdomen is always collapsed and is often fragmented into tiny pieces which are plastered into the front surface of the balloon. One may conclude that in this stage the prey still serves as the stimulus for the male to construct the complex balloon inasmuch as he always begins by catching the prey. But certainly the prey no longer serves as food for the female; moreover, because of its minute size and the fact that the female pays no attention to it while in the process of manipulating the balloon, it would seem that it has entirely lost its significance in courtship. It may be assumed, therefore, that in this stage the balloon remains as the sole stimulus for copulation. (Fig. 3.)

Stage 7 is well illustrated by *Empimorpha geneatis* Melander, a species which in 1946 I discovered was a balloon-maker. This was the species which initiated my study of balloon flies, and these early observations were published a year later (Kessel and Karabinos, 1947). One morning, while looking out of our kitchen win-

UNIVERSITY OF MICHIGAN LIBRARIES

dow, I observed a number of conspicuous white objects scintillating in the morning sunshine as they zigzagged back and forth close by a Monterey pine. They were flying at an altitude of some fifteen or twenty feet, and it was only by tying my net handle to a sturdy surf-casting rod and then mounting to the top of a six-foot stepladder that I was able to bring any of the specimens to net. They proved to be all males and the white object which each carried was a delicate, balloon-like structure which invariably had a minute dipteran or hymenopteran plastered into its anterior surface. When swept roughly into the net the flies invariably drop their balloons, but when care is exercised and the stroke of the net is gentle and true, they sometimes retain possession of these structures and can be transferred to a container while still grasping them tightly. As a rule these balloons are somewhat flattened, suggestive of the flattened structures already mentioned in connection with the introductory comments about *Hilara sartor*. In *E. geneatis*, however, the prey is always present although crushed and dry and so invariably unfit for food. These minute captured insects are always oriented so that the head, and often the thorax as well, projects free from the balloon, being directed forward and upward. And this projecting part of the prey's body is used as a handle which the male always seems to have hold of with one or more of his feet. In addition, these insects sometimes have the tarsi of two of their legs hooked together under the balloon. I was able to ascertain that the eligible bachelors of this species do not discard their balloons when they retire, unsuccessful from the standpoint of marriage, from the morning dance. Such a male keeps his balloon for another try at mating the following day, although he is able to make another, smaller balloon, in case the first is lost.

During the first years of my study I was able to observe the mating activities of this species. On several occasions I saw a female join the dancing group of males and select a mate. As the two embraced they lost altitude for a moment, and then floated off together to settle on nearby vegetation. Examination of the paired flies revealed that the balloon had been transferred to the female. In the act of mating the male hangs from the vegetation by his front feet, his middle legs supporting the female's thorax, and his hind legs holding her abdomen. The female holds onto the balloon with all of her feet; never does she grasp the prey as a handle for the balloon in the manner of the male. Instead, she keeps turning the balloon from one position to another during the mating period, apparently entirely unconcerned with the prey and certainly making no attempt to feed on it. This tiny insect is absolutely unfit for food; its abdomen is always ruptured and plastered into the balloon's surface. In fact I am of the opinion that *E. geneatis* has ceased to capture prey for food in the manner of its ancestors. Never did I find flies of this species in possession of prey other than the tiny ones crushed into the balloons, whereas again and again I have found them feeding on manzanita flowers. Each time they were observed, the fly was obtaining nectar through a puncture which it had made through the corolla with its proboscis. Here, as on all other occasions when the males were observed alone, they were carrying their balloons with them.

Stage 8: In this last stage of the evolutionary sequence the male no longer needs to capture a prey in order to be stimulated to construct a balloon. So the gift package includes no prey whatever, not even a dried-up, inedible one such as is present in stages 6 and 7. I have not yet had the opportunity to study any of the species representing this last stage, but *Hilara sartor,* which was discussed at the beginning of this paper, is an example. One cannot blame Osten-Sacken and his colleagues for some of their wild speculations as to the significance of the balloons of this species, for these forms were entirely without prey and the earlier stages in the evolutionary sequence of these breeding-

behavior patterns were not yet recognized, let alone understood. Another fly which represents this eighth stage is *Hilara granditarsus* Curran which Melander (1940) observed carrying balloons in Alberta. As in the case of *H. sartor* there was of course no prey included in the gift package.

Source of the Balloon Material

In addition to the debate about the significance of the balloons there has been much speculation as to the source of the material from which the balloons are constructed. It will have been noted that I am convinced that in the two species of balloon flies which I have studied the balloons are constructed from secretions of anal glands which are either applied in the form of globules or are drawn out to produce silklike threads. The idea of the anal origin of the balloon material is not imcompatible with the chemical nature of the balloons (Kessel and Karabinos, 1947). Our investigation revealed that this substance consists chiefly of a mucoprotein allied to gastric mucin. However, Melander (1940) suggests that both the rudimentary webs with which certain empidids entangle their prey, and the more complex balloon structures produced by others, are formed from a viscous secretion of the proboscis as the fly jabs this organ again and again into its victim to quiet it. He says, "The prey is enveloped by the male in a froth secreted by the proboscis so that it becomes more enticing to the female."

Eltringham (1928) and his colleague Hamm (1928) were likewise convinced that the silk of these flies came from the salivary glands, although they were willing to grant that the globules used in balloon construction by some species might have a different origin; they suggested that the flies might collect the material for the globules from homopterans, for example. But Eltringham and Hamm, whose studies incidentally were confined to species of the genus *Hilara*, became intrigued by the enlarged basal segments of the foretarsi of the males of these forms. These structures reminded them of the swollen foretarsal segments of Embioptera, which, in this order of insects far removed from the Diptera, are the source for the silk used to line their tunnels. Eltringham made dissections and claimed to have demonstrated that these foretarsi of hilaras contain silk-producing glands. While this may be true (and I have made no histological studies to confirm or disprove this point), the mere existence of such glands would not determine that the silken-thread forerunners of empidid balloons or the balloons themselves come from tarsal-gland secretions as Eltringham and Hamm supposed. To my knowledge no one has yet seen a balloon fly constructing its balloon, and it seems logical to assume that both the evolutionary primordia or silken webs with which certain empidids entangle their prey and the complex balloons which follow them in the evolutionary sequence must be produced by homologous structures. The theory that these webs and balloons are formed from secretions of the foretarsal glands is further weakened by the fact that certain species of *Hilara* which possess the largest and most swollen foretarsi neither make balloons nor entangle their prey in webs. Moreover, the empidids which make the largest and most complex balloons belong to other genera and do not have the foretarsi enlarged at all.

The flies which constitute the family Empididae were segregated into this taxonomic assemblage on strictly morphological grounds and therefore without benefit of the knowledge of their web- or balloon-making activities, yet it is only among the members of this family that we find balloons produced. If members of widely different families—for example, a group of muscids and a group of nematocerans—should likewise produce balloon-like structures, we would not be disturbed if it were claimed that nonhomologous

UNIVERSITY OF MICHIGAN LIBRARIES

structures produced the material for the balloons in the different groups, for it would be obvious that they had acquired the balloon-making habit independently. But to suppose that the balloon-producing substance in the one family, Empididae, is produced in some cases as a froth of the salivary glands, in others as a secretion of the glands of the foretarsi, and in still others as a secretion of the anal glands, seems unreasonable. I feel that it is necessary to assume that the evolutionary sequence of courtship patterns involving balloons or balloon-like structures was the result of a continuity of function of homologous structures, and my own studies have convinced me that, in the two species which I have studied extensively, the balloon material, for both the globules and the silken threads, must come from anal glands.

REFERENCES

ALDRICH, J. M., and TURLEY, A. L. 1899. A balloon-making fly. *Amer. Nat., 33*:809–812.

BECKER, T. 1888. *Hilara sartor* n. sp. (Osten-Sacken in litt.) und ihr Schleier. *Berlin Ent. Ztschr., 32*:7.

ELTRINGHAM, H. 1928. On the production of silk by species of the genus *Hilara* Meig. (Diptera). *Proc. Roy. Soc. London,* Ser. B, *102*:327–334.

HAMM, A. H. 1928. On the epigamic behavior of *Hilara maura* Fab., and two allied species. *Proc. Roy. Soc. London,* Ser. B, *102*:334–337.

KESSEL, E. L., and KARABINOS, J. V. 1947. *Empimorpha geneatis* Melander, a balloon fly from California with a chemical examination of its balloons (Diptera; Empididae). *Pan-Pac. Ent., 23*:181–192.

KESSEL, E. L., and KESSEL, BERTA B. 1951. A new species of balloon-bearing *Empis* and an account of its mating activities (Diptera: Empididae). *Wasmann Jour. Biol., 9*:137–146.

MCATEE, W. L. 1909. Some habits of Empididae. *Ent. News, 20*:359–361.

MELANDER, A. L. 1940. *Hilara granditarsus,* a balloon maker. *Psyche, 47*:55–56.

MIK, J. 1888. Ueber ein spinnendes Dipteron. *Verhandl. K. K. Zool.-Bot. Gesell. Wien, 38*:97.

OSTEN-SACKEN, C. R. 1877. A singular habit of *Hilara. Ent. Monthly Mag., 14*:126–127.

POULTON, E. B. 1913. Empididae and their prey in relation to courtship. *Ent. Monthly Mag., 49*:177–180.

VERHOFF, E. 1894. Zur Biologie von *Hilara. Ent. Nachr., 20*:1–2.

EDWARD L. KESSEL is Professor of Biology at the University of San Francisco and Associate Curator of Insects at the California Academy of Sciences.

Evolutionary Trends in the Courtship and Mating Behavior of Salientia

D. L. JAMESON

THE mating behavior and particularly the courtship activities of frogs and toads are frequently described as unimaginative. A casual look at the literature will inform one that in most species the male, at the beginning of the breeding season, precedes the female to the pond, emits his particular distinctive call, and clasps by one of two means the first object of the appropriate size, texture, and silence which approaches. The rule is: if it is not small enough to eat nor large enough to eat you, and does not put up a squawk about it, mate with it. With these enlightening details we should feel we know sufficient about frog courtship and would turn to more fruitful pursuits. The nonspecialist may be excused for lack of further interest, but professional herpetologists, including the present writer, have frequently been inclined to disregard frog courtship.

Boulenger (1886*a*) classified the oviposition of salientian eggs and later (1896–97) discussed the types of amplexus in European forms. Sampson (1900) reviewed the literature on unusual modes of both breeding and development. Noble (1925*a*, 1925*b*, 1927) attempted to trace phylogeny in both Salientia and urodeles by the use of life-history data. Noble and Aronson (1942 and elsewhere) have made very detailed laboratory studies of mating behavior in some Salientia, but field observations are both scattered and incomplete. Lutz (1947, 1948) discussed the evolutionary trends found in the care of salientian eggs. Orton (1949, 1951, in press) discussed the evolution of larval stages.

Some information on several salientian families is brought together in this article in an attempt to discern both tendencies and generalities of mating behavior and particularly of courtship. Mating behavior may include all aspects of the activities of either or both parents that result in a successful production of offspring. Courtship may, for our purposes, be defined rather broadly to include those of the mating activities which involve the relationship of the parents to each other. We may note that the unusual is frequently described in the literature in detail while the common situation is more often ignored. Thus considerable bias has been difficult to avoid.

Survey of Families

Ascaphidae

Slater (1931) and Noble and Putnam (1931) give detailed accounts of mating behavior in the American bell toad, *Ascaphus truei*. The voiceless male swims about on the bottom of rapidly flowing streams in search of a mate. If he grabs another male he will soon release his hold, even if the grasped male does not struggle. When the male encounters a female he grabs the handiest portion, usually a limb, and immediately obtains a secure grip. He then places the axis of his body at right angles to that of the female and throws the female on her back. This action produces a "tonic immobility" on the part of the female, and this allows the male to obtain a pelvic amplexus interdigitating his fingers along the ventral sacrum of the female. The female straightens her hind legs forming a narrow V, and the male then flexes his back so the pelvis is

UNIVERSITY OF MICHIGAN LIBRARIES

at right angles with the backbone. The blood-vessel-rich tail appendage of the male, supported by two cartilaginous elements, is flexed at right angles to the pelvis, parallel to the backbone and pointing anteriorly. The thrust of the tail appendage into the cloaca of the female causes her to bring her legs together, apparently in an attempt to escape. This action, along with the spines of the male appendage and those on the legs of the female help to maintain the appendage in position in the cloaca. The sperm is transported to the cloaca by means of the appendage. The eggs when deposited are directed downward by the smaller cloacal appendage of the female, and they adhere to rocks on the bottom of the stream. Neither worker mentions whether or not deposition of the eggs occurs during amplexus but their description of laying and development, and the fact that sperm has been found in the cloaca of the female (Noble, 1925), suggest that amplexus is not necessary for deposition.

The only known relative of *Ascaphus*, the New Zealand bell toad (*Leiopelma*), lays its eggs on land and has direct development (Archey, 1922). Descriptions of mating and deposition in this form are lacking.

Pipidae

According to Bartlett (1896) the male Surinam toad, *Pipa americana*, clasps the female inguinally; the coupling occurs in water. The cloaca of the female is everted and protrudes dorsally forming an ovipositor. By pressing this lightly from side to side and forward with his body, the male works the eggs through the ovipositor, extruding them one at a time into the pouches of the female's back. Another account (Fermin, 1765) indicates that amplexus occurs on the bank and that the eggs are laid on the ground. The male then places the eggs on the female's back, but the account gives no details of how the male accomplishes this feat.

Bles (1905) was able to induce the South African clawed toads, *Xenopus laevis*, to breed in the laboratory by feeding them regularly through the summer, lowering the temperature during the winter, and again raising it in the spring. The draining off, cooling, and re-adding of water to the aquaria to simulate rain also helped. He found that the males begin to call in the spring, gradually increasing in volume and frequency. At the time of mating the male makes a sudden dash, grabs the female in the inguinal region, and then changes the tone of his call. At each uttered note the male strokes the underside of his head against the back of the female. When eggs appear the male becomes silent, but will call again if oviposition stops. Each egg appears separately and is held by the female's cloacal lips. The female then grasps a leaf or twig with her hind limbs. The egg is released sharply by the cloacal lips and is propelled along a shallow median groove on the ventral surface of the male, over the cloaca of the male, and then to the weed where it becomes attached. A gentle water current is created by the swimming motions of the male, and this probably helps the egg to move along its path.

Discoglossidae

The mating behavior of the obstetrical toad, *Alytes obstetricans*, has been detailed by De L'Isle de Dreneuf (1876). The male calls from small holes dug in the ground, and mating occurs on the ground nearby and lasts most of the night. The male clasps the female tightly around the head above the forelimbs. Immediately preceding ovulation the male moves his legs forward so that his heels are together, anterior to and above the cloaca of the female. As the first eggs are emitted the male catches them in his feet and by stretching his legs posteriorly delivers the 20 to 60 eggs. The male then moves his legs anteriorly and laterally, entwining the eggs around his legs. The eggs are carried for several weeks until the tadpoles are ready to hatch, at which time the male makes a brief visit to water where the developing individuals are left

to finish their life cycle. The male is reported (Boulenger, 1912) to select a pool where tadpoles are not already present.

Another member of this family, the yellow-bellied toad *Bombina maxima,* has no vocal sac but according to Liu (1950) is able to make slight sounds. Mating occurs in water; the male clasps the female just in front of the base of the thighs, and the eggs are laid in small masses which sink to the bottom of the pools or are suspended on vegetation.

Rhinophrynidae

The Mexican burrowing toad, *Rhinophrynus,* will call from his burrows, but the eggs are laid in water and develop into aquatic larvae (Orton, 1943). Stuart (1935) reports that the courtship is aquatic and that amplexus is inguinal.

Pelobatidae

The spadefoot toads (*Scaphiopus*), according to Bragg (1944, 1945), will call, beginning about dusk, from small burrows dug in the banks of ponds. The males leave these burrows during the evening and move into the water where they contribute to the ever-increasing chorus. The males of some forms (*S. hammondi* and *S. holbrooki hunteri*) are very active and swim about vigorously in deeper water, occasionally coming in contact with other frogs, when the males will paw briefly with one another. The male will give a warning cry if clasped by another male, and will then quickly be released. Other forms (*S. bombifrons* and *S. holbrooki holbrooki*) float passively in deep water, while still other species (*S. couchi*) frequently call from the bank or from very shallow water near the bank. The active forms will break off calling and pursue any female that approaches. The passive forms apparently ignore the female until touched. The clasp is inguinal, and the eggs are laid attached to vegetation in the water, where they develop rather rapidly. Breeding typically occurs in temporary water.

The males of the Old-World pelobatid, *Scutiger schmidti,* call in the daytime but the intensity of the call increases at night. The females are apparently courted by the males, as Liu (1950) on three different occasions found three males calling from stations next to and around a female. When the female selects a male the clasp is pelvic, with the male's right hand over the left hand and all fingers bent. The method or basis for selection is not indicated. Mating occurs under bamboo roots, with the pair moving to small mountain streams for the deposition of the eggs. The male has two nuptial patches on his chest which he apparently uses to stimulate the anal region of the female. Similar nuptial patches appear generally in Old-World pelobatids, and in many other groups.

The male parsley frog, *Pelodytes punctatus,* clasps the female with his arms tightly around her pelvis, brings his elbows together, and places his forearms parallel along the female's mid-ventral line. (Boulenger, 1896.)

Rhacophoridae

The male Chinese tree frog, *Rhacophorus leucomystax,* has two very distinct calls, but the significance of these calls was not determined by Liu (1950). The male calls from the bank of a pool while the female is approaching and then he clasps her above the armpits (supra-axillary position), lying very close to the female. The female moves about until she finds a suitable locality along the bank near water for depositing her eggs. She then flattens her body and moves her legs medially and laterally. The male bends his vent down next to the cloaca of the female and moves his hands into her armpits. The first and second fingers are pointed backward and downward, the third and fourth anteroventrad. The male places his feet and tarsi between the thighs of the female and remains passive. The female produces foam from the vent and beats it well with her hind legs and feet by medial and lateral movements of her legs, rotating them as they cross at the mid-line. She then bends her thigh to

UNIVERSITY OF MICHIGAN LIBRARIES

raise the posterior part of her body, and the vent emits the eggs along with considerable fluid which the female beats into foam with tarsi and feet. When the eggs appear, the male may gently move his legs up and down.

Rhacophorus bambusicola has an amplexus like that of *R. leucomystax,* while in *R. omeimontis* the second finger of the male is sometimes placed on the dorsal basal part of the female's arm. *R. leucomystax* and *R. bambusicola* lay their eggs in various places on the ground near water, while *R. omeimontis* spawns on tree leaves overhanging the water. In these cases the eggs develop in the foam mass until they hatch, when the larvae wiggle or fall into the nearby water. Another *Rhacophorus* (*R. reticulatus*) has been described as carrying the ova, which adhere firmly to the abdomen (Sampson, 1900).

The male *Polypedates dennysi* utilizes an axillary clasp with his feet together, the dorsal surface of the feet being pressed against the posterior part of the female's body. The female pats the surface of a leaf with her hind feet until the eggs are deposited against the male's feet, following which the male slides his feet dorsally against his own body and then returns to the original position. As the eggs are laid in small groups, the foam is well beaten by the patting of the female's feet into a large leaf-nest mass overhanging the water. (Pope, 1931.)

Ranidae

The mating behavior of the common leopard frog, *Rana pipiens,* has been described in some detail by Noble and Aronson (1942, 1945). The male has three calls: a regular sex call, used when calling from the mating site; a warning call, used when clasped by another male; and a sex-warning call, which is used by the male when he is about to clasp a female. The female also has a warning call that is used to discourage males when she has not ovulated.

When mating, the male approaches the female, swims vigorously about her, and emits his sex-warning call which appears to calm the female. He then clasps the female pectorally, his back arches slightly, and his ventral surface adheres closely to the back of the female. After a short time the female performs what is called "backward shuffling" which alternates with rest periods for about one hour. The oviposition posture, in which the female spreads her thighs and places her heels together and the male raises his knees and places his feet on her thighs, is assumed just before the eggs are deposited. The eggs are deposited in small clusters during a process referred to as an "ejaculatory pump," which is repeated until the female is spent. The steps in the "ejaculatory pump" are as follows: the female contracts her abdomen; the male spreads his legs and arches his back, drawing the cloaca forward; the female arches her back; the male straightens his back and presses his legs against the female's abdominal wall. This brings the cloacas together briefly at the instant when 10 to 23 eggs are emitted into a triangular area formed by the legs of the pair. Mating behavior in other species of *Rana* has been described by Aronson (1943*b*, 1943*c*). They are all basically similar. *Rana catesbeiana* and *Rana clamitans* differ from *Rana pipiens* and *Rana septentrionalis* in that the female extends and the male flexes the hind legs slightly more, and the male lies slightly further anteriorly on the female during amplexus. This will tend to raise the cloaca and is perhaps associated with the surface-film egg-masses of *Rana catesbeiana* and *Rana clamitans.*

Nest-building habits have been adopted by *Rana adenopleura* (Liu, 1950). The male, using his nose as a digger, builds a nest burrow in the margin of a pool. The males call in a chorus from their holes until a female approaches one of the males, at which time the male turns toward the female and calls again, adding a series of low unmusical notes. This last note is taken up and continued by all males in the vicinity until the female approaches her

mate, at which time all the males return to the original note. Following amplexus the eggs are laid in the nest where they receive some protection by being isolated from the insects of the pond. *Rana episthodon,* of the Solomon Islands, is reported (Boulenger, 1886*b*) to have direct development, but its mating habits are unknown.

The Chinese ranid, *Staurois chunganensis,* has been described in some detail by Liu (1950). The male is very active and calls with a cricket-like note from stones, trees, and the banks of mountain streams. If a male encounters, and is clasped by, another male he will croak and kick violently, obtaining his release. The female on the other hand is passive when first clasped. The clasp is axillary with the fingers curved up at the posterior-lateral angle of the female's coracoid. Shortly the female carries the male, jumping from stone to stone until she finds a suitable quiet pool in a stream. Near or under a rock in the water the female lowers her head and raises her vent, pressing it against the stone several times. The male and female then form a triangular space with their legs, and the eggs are deposited into this triangular area and fertilized. The vent of the female is then used to attach the eggs to a stone. The female obtains her release from the male by elongating her body, shaking her hind limbs violently, and arching her body downward. The male frequently croaks "in complaint" but soon releases her. This is very similar to the release mechanism of the female *Rana planeyi* as described by Liu (1930).

Microhylidae

The data are relatively inadequate for this group. In Florida the writer has observed the narrow-mouthed toad, *Microhyla carolinensis,* calling from small holes in the bank of a ditch about 15 inches above the water. One male called vigorously despite the presence of a bright flashlight, and another frog came from the water and crawled up the very steep bank. The first individual continued his calling, ignoring the approaching frog while the latter moved completely around him. When the invader touched the calling frog he immediately turned and clasped the second frog. The second frog then carried the male carefully down the steep bank to the water's edge. When they were collected the second frog was found to be a female. Anderson (1954) reports that these frogs call in a choral pattern from rather fixed positions. The male responds to the approach of another individual only by increasing the calling rate. Amplexus is semi-pectoral or axillary depending on size, with the male's arms posterior and ventral to the female's axilla and his palms turned outward and forward. Sex recognition may be due to a faint vibration on the part of the clasped male. Some change in the quality of the call occurs approximately at the time of amplexus. The male calls while clasping the female, and the pair cooperately swim about sometimes in brief, jerky movements until shortly preceding oviposition. The male then flexes his thighs, with the shanks turned dorsolaterally and the feet laterally and anteriorly. The female raises her hind limbs and vent region to the surface of the water and moves her knees laterally, "swaybacking" the body. At the time of oviposition the female extends her legs ventro-laterally, bringing the cloacas above the water-surface. The male slides forward so that his vent is about one-eighth inch anterior to the vent of the female and brings his feet together behind and under the female's cloaca, curving around her buttocks. The eggs are then deposited in groups of approximately 30. The female leaves the water immediately following deposition, which may stimulate the male to release his clasp.

Hylidae

Very excellent studies on the tree-toad, *Hyla andersoni,* have been made by Aronson (1943*a*) and by Noble (1923). The male calls from a tree or in or near a pond until touched by the female. Frequently

the females find it necessary to "bump" or even jump on the male. Eventually the male clasps the female with a supra-axillary grasp, and if in a tree the male then rides the female to the pond. In the water both sets of hind limbs are fully flexed. After some time the female extends her hind limbs, depresses her back, and contracts her abdomen. The male then partly extends his hind legs, slides forward, and arches his back, bringing the cloacas together at the instant that 8 to 10 eggs are extruded. The male and female then return to the flexed-legs position, and the eggs fall to the bottom of the pond. This is repeated until the female is spent, when she will arch her back sharply, throwing her head dorsally, and obtain her release. Smith (1940) gives a similar description for *Hyla regilla,* except that this species probably does not mate in trees.

The South American tree frog, *Phyllomedusa guttata,* has a very interesting mating behavior which has been described by Lutz (1947). The male has a double-cluck mating call which he emits while on the limb of a tree. The female is clasped in the axillary position for about 24 hours during which she moves about selecting a leaf hanging over water on which to deposit her eggs. She settles on the upper side of a leaf, over and parallel to the median leaf rib, with feet extending over the edge to the underside of the leaf. While spawning, the pair moves slowly forward from the tip toward the stalk, folds the leaf into a nest, and fills it with eggs and foam. The two ends of the leaf are left open. When spawning is finished, the male calls a series of single clucks and releases the female. Some pairs may continue on another leaf if the female is not spent. The eggs develop into tadpoles, which fall out of the hole in the end of the leaf nest and into the water below. Noble (1925) and Lutz (1947) have pointed out that some Hylidae carry their eggs on their back (*Hyloscirtus goeldi*) while still others build aquatic nests (*Hyla rosenbergi, Hyla faber*).

Bufonidae

Three calls have been described by Aronson (1944) for the males of the eastern North American toads (*Bufo americanus, B. terrestris, B. fowleri*). These include a sex trill which is very loud, a warning vibration which is very quiet, and a small chirp the function of which is unknown. Amplexus is frequently supra-axillary, especially if the male is very small, otherwise it will be axillary. After a short time the female becomes slightly restless, and abdominal muscles begin peristaltic-like movements. The female arches her back concavely and extends her legs caudally with her heels together. The male then arches his back still more convexly, bringing the cloacas together. This is followed by a contraction of the female's abdominal muscles which issues the eggs. The male's abdominal wall constricts several times and the female then begins to move about, laying the eggs in strands.

Liu (1950) described the mating behavior of the Chinese toad, *Bufo gargarizans.* The male appears first and calls from the ponds until the females enter and are clasped in the axillary position. The female lowers her toes to the bottom of the pond and the male places his hind legs between the legs of the female, the pair thus being in an upright position. The eggs are laid in strings which are stretched over a considerable area as the female walks along the bottom.

Firschein (1951) has described an interesting behavior in *Bufo nayaritensis.* The male clasps the female in an axillary embrace and places the plantar surfaces of his hind feet on the dorsal surface of the hind feet of the female. At irregular intervals the body and shanks of the male will convulse and the female will emit a low chirp, to which the male responds by thumping his fourth hind toe against the foot of the female.

Leptodactylidae

The male leptodactylid, *Syrrhophus marnocki,* has two calls (Jameson, 1954):

a social call, given as a member of a choral group, and a breeding call, which is emitted only when the female is present. The male uses his social call until the female appears, when he begins to give the breeding call, which he continues constantly until amplexus occurs and then intermittently until he releases the female. Before amplexus the male scratches the back, neck, and legs of the female with his hind legs while the female moves about him. When the female stops, the male completes an axillary clasp and continues to stimulate the female with his hind legs. The female digs a trench with her front legs and deposits the eggs as the pair moves along the trench; both male and female utilize their hind legs to cover the singly deposited eggs with dirt as they move. When the 8 to 20 eggs are laid the male releases the female and ceases to call.

According to Mulaik (1937), a small rounded cavity is formed in the ground by the male *Leptodactylus labialis*. He returns to this cavity nightly and calls until a female arrives, and the eggs are laid in a frothy mass. Amplexus was not observed. *Syrrhophus* and some *Leptodactylus* have direct development.

Dendrobatidae

According to Dunn (1941), *Dendrobates auratus* males call frequently and move about on the ground, leaves, and rocks with considerable vigor. The calling male is soon followed by several females which compete with each other to come in contact with him. If the females fall behind, the male will pause and become more vociferous. The male finally disappears beneath some leaves, followed by one female, the others having dropped out along the way. Amplexus has not been observed but the union results in the deposition of one egg which the male attaches to his back and retains as it develops into a tadpole, at which time the male will take the egg either to the water of a pond or more frequently to the water in a tree hole.

Atelopodidae

The male *Rhinoderma darwini* carries his eggs in his vocal pouch until the young hatch fully formed. Further details of the life history are unknown. (Sampson, 1900; Orton, 1951.)

Discussion

The information presented here reveals some noticeable evolutionary tendencies and emphasizes some of the major gaps in our knowledge of mating behavior in Salientia. Where clear-cut tendencies are not evident it is often easy to think that they do not exist. However, information obtained for one species or even for one subspecies is not necessarily applicable to other forms. Because of this, generalization can only be tentative, and always subject to both exception and discard. More extensive review of particular aspects (e.g., calls) is certainly needed in several cases. An over-all review of the problems and processes of mating behavior, in an attempt to arrive at both generalities and evolutionary tendencies, may be approached at this time.

The actual factors which stimulate the amphibian to breed are unknown. Undoubtedly they differ in the various forms. A cyclic anterior pituitary-gonadal hormone reflex has been suggested for many species and is fairly well demonstrated in *Rana pipiens* (Rugh, 1935, 1937; Noble and Aronson, 1942) and *Xenopus laevis* (Shapiro, 1936*a* and 1936*b*, 1937; Berk *et al.*, 1936). Considering that these species are not closely related and that a great number of other vertebrates have demonstrated a comparable sexual cycle, it may be safe to assume that this is a general phenomenon. Rugh (1937) has shown that the pituitary-gonadotropic hormones are not species specific, although some phylogenetic limitation of gonadal activity has been noted (Creaser and Gorbman, 1939; Rugh, 1948). Since *Bufo* is very sensitive to mammalian pituitary extracts while *Rana* is not, more extensive data may prove fruitful in demonstrating phy-

UNIVERSITY OF MICHIGAN LIBRARIES

letic relations in the Salientia. The relationship of the pituitary-gonadal cycle to environmental factors is undoubtedly different in each species.

It was early realized (Boulenger, 1896, 1912) that the term "breeding season" was completely inadequate. Boulenger (1896), Fletcher (1889), Bragg (1940*a*), and others have attempted to classify breeding seasons. Generally these divide the species into those that breed during any warm rain at any time of the year and those that breed only at about the same time year after year. Bragg (1940, 1945) calls the first of these a xeric breeding pattern, the second a mesic pattern, but indicates that intermediate species occur. Only the observance of deposition or of freshly laid eggs can accurately delimit the times of actual breeding. The activities which precede and follow amplexus may extend the "breeding season" over several months, while actual mating occurs only on a few scattered nights during this period (e.g. *Hyla regilla,* Jameson, in press). The males are more sensitive to the hormone release (Creaser and Gorbman, 1939) and thus will usually call before the female enters the pond and frequently remain long afterwards. Thus the observation of calling males does not necessarily indicate the breeding season (Littleford, 1946). There is a tendency for some desert species (*Scaphiopus*) to breed at any time during rains (Bragg, 1941, 1945). Several species may utilize a pond to breed separately during one year, all together another year, and variously in other years, as has been noted by many workers (Carr, 1940). Noble and Aronson (1942) pointed out that captivity rapidly reduces sexual activity.

The hormone cycle probably reaches a regular peak at about the same time each year. The question then remains, does the environmental situation produce a final impetus to the hormonal cycle in the physiological sense, or does it serve as a passive and mechanical outlet for reproductive behavior? The first alternative is certainly suggested in some cases (several Florida species, Carr, 1940; *Bufo* and *Scaphiopus,* Bragg, 1941; *Rana,* Noble and Aronson, 1942; *Xenopus,* Berk, 1938), but such activity would be very obscure where the environmental situation is stable and sudden changes are not apparent, as in the completely aquatic courtship activity described for *Ascaphus* (Noble and Putnam, 1931). Bragg (1941) suggests that some frogs do not normally ovulate except during amplexus. Female *Hyla regilla* have not ovulated at the time of migration to the breeding pool and will permit amplexus while in this state, and Anderson (1954) reports that *Microhyla carolinensis* does not ovulate until amplexus. Shapiro (1936*b*) has clearly demonstrated that mating, ovulation, and oviposition are independent factors in *Xenopus.* However, Noble and Aronson (1942) have demonstrated that *Rana pipiens* will not allow amplexus until after ovulation is almost complete. The specific environmental factors at work, and how they operate, are thus important. Temperature (Barbour and Walters, 1941; Wright, 1914), humidity (Cummins, 1920; Berk, 1938; Noble and Noble, 1923), rain (Fletcher, 1889; Bragg, 1941), algal content (Savage, 1935), and ground moisture (Carr, 1940; Jameson, in press) have been suggested for various species. Wasserman suggests that hurricanes producing low barometric pressure may be required to induce breeding in *Scaphiopus h. holbrooki,* and the evidence is very favorable for this assumption (personal communication; see also Berk, 1938).

The same factors which are responsible for initiation of breeding activity must contribute to the migration of many species, particularly those that breed in temporary situations. Bogert (1947) has suggested that a few toads enter a pond at random and that their calls attract other individuals to this situation. Goldschmidt (1926) has demonstrated that both sexes of *Scaphiopus hammondi* are stimulated by calls from a breeding chorus of the same species. The work of Blair (1942) with eastern North American *Bufo* would

support this assumption. On the other hand, Cummins (1920) demonstrated that four species of Salientia move to the pond without regard to choruses and actually arrive and aggregate before calling commences. Savage (1935) has also demonstrated that *Rana temporaria* gather in silence. This suggests some inherent tendency of the animals to return to a home pond. This is supported by the recovery of marked tree frogs (*Hyla regilla*) in the same part of the pond where they had been the previous year (Jameson, in press and additional data). This frog also appeared, in January 1955, in one pond in great number before calling began, while in another pond at least a few individuals called sporadically during the formation of the chorus. Further suggestions of inherited tendency to spawn in a given site are found in *Microhyla carolinensis,* which returned to a particular site and formed a chorus even though the original pool had been filled (Anderson, 1954). Maynard (1934) found that *Bufo americanus* followed regular migratory paths to breeding ponds.

In many Salientia the calls are certainly one of the most significant aspects both of the individual and of the species. Noble (1931) felt that smaller species have shriller voices, that larger ones have deeper voices, and that temporary-pool breeders were louder than permanent-water forms. This is far from universal but it is perhaps worthy of consideration. Many kinds of calls have been described, including (1) the sex call or trill, produced by males at the breeding site; (2) the warning call and warning vibration, used in defense against both predators and emotionally active males; and (3) the female warning call, used in defense and sometimes when ovulation has not occurred. The male chirp and several other calls without known function have been noted. The sex-warning call of some *Bufo,* the sex trill of *Syrrhophus marnocki,* and a peculiar sex call of *Microhyla carolinensis,* are used during the actual mating. *Phyllomedusa* has a release call given after the eggs are deposited. Dr. W. F. Blair (personal communication; Blair and Pettus, 1954) is recording amphibian calls and converting them to sonograph records which show the sounds as patterns of lines on a chart. Related species have similar patterns indicating affinities which may ultimately demonstrate phylogenetic trends.

Where studies have been made, many species have a somewhat elaborate courtship behavior with the calls. Choral groups have been described in ten species (*Hyla crucifer,* Goin, 1948; *Hyla regilla,* Jameson, in press; *Syrrhophus marnocki, Eleutherodactylus latrans,* Jameson, 1954; *Microhyla carolinensis,* Anderson, 1954; *Rana clamitans,* Martof, 1953; *Rana nigromaculata,* Liu, 1931; *Rana adenopleura, Hyla annectans, Scutiger schmidti,* Liu, 1950) and have been broadly hinted at in many others. This may well be a universal trait in the voiced forms. The presence of a choral pattern, such as that described by Goin (1948), where each of three individuals calls closely and regularly following each other and where each uses a different note, would certainly suggest that the frogs are aware of each other and can hear each other. Since these and other *Hyla* will consistently perform this choral pattern from trees, and since *Syrrhophus* and *Eleutherodactylus* call only from terrestrial situations, it seems probable that the frogs are not only able to hear each other through air vibrations (see also Courtis, 1907; Yerkes, 1905) and recognize the particular call of their species, but that they are also able to distinguish the calls of the several different individuals in their own choral group. However, Blair (1947) was unable to demonstrate that two species of *Scaphiopus* could recognize their own calls when given a choice. Martoff (1953) has suggested that the recognition of individuals in the choral group is a part of the establishment of definite territories or at least spheres of influence in *Rana clamitans.* Bragg (1944) indicates that active movements of male *Scaphiopus,* constantly moving toward, and coming in contact

with, each other and then moving away, result in each individual's remaining in his particular area. This may be an indication of at least a home range. Further illustrations of home ranges are indicated by the persistent reappearance of individuals both night after night and year after year at the same place, although many of these observations are not of marked individuals. *Syrrhophus marnocki, Hyla regilla,* and apparently *Hyla crucifer* and others, establish home ranges independent of the breeding season (feeding ranges?) so that the establishment of calling sites by male frogs and toads during the mating season may be a general species characteristic rather than a breeding phenomenon.

The selection of mating and breeding sites has received considerable attention from those workers who have studied mating in the field. The more primitive conditions may be those that are found in the purely aquatic breeders such as *Rhinophrynus, Ascaphus, Bombina, Xenopus, Scaphiopus, Bufo,* and most *Rana.* Intermediate conditions are found in *Scutiger, Staurois,* and some *Hyla* and *Microhyla,* where courtship and coupling are terrestrial activities while spawning occurs in the water. *Alytes* and *Dendrobates* mate and spawn in terrestrial situations but carry the tadpoles to water. *Rhacophorus* and *Phyllomedusa* mate and spawn in terrestrial situations, depending on rain to transport the tadpoles to water, while *Alytes, Dendrobates,* and some *Hyla* purposefully carry the tadpoles to the proper places for future development. In *Syrrhophus, Leptodactylus,* and *Rana opisthodon* development is entirely within the nest, while in *Leiopelma* (Archey, 1922) and *Eleutherodactylus* (Lynn, 1942 and others) one or the other of the parents remains near the nest during development. *Pipa, Nectophrynoides* (Orton, 1949), and *Rhinoderma* are at the other extreme and carry the developing embryos until they transform. One may wonder if *Pipa* developed this characteristic in a terrestrial situation and has since returned to water.

The preparation of the breeding site appears limited to those forms which have some nesting habits designed to protect the developing embryos. The place of call of the male appears to determine the breeding site in most species but we have seen above how *Staurois, Phyllomedusa,* and sometimes *Hyla* and *Microhyla* sites are selected by the female after the first stages of mating are completed. The female *Bufo cognatus* may (Bragg, 1937) select a likely mating pond and wait there for the males to come to her rather than moving to nearby ponds where males are calling. If the males do not find mates the first night, they move to other ponds.

In those species which have a voice, the call is perhaps the most important part of sex recognition. Noble and Aronson (1942), Aronson (1944), and others have shown that in several species (*Xenopus laevis,* several *Rana,* and several *Bufo*) the females will not emit the sex-warning chirp or tick during the height of pituitary activity. Touch (*Hyla andersoni,* Noble and Noble, 1923); chemical sense and difference in color (*Rana sylvatica,* Banta, 1914; *Bufo,* Savage, 1934); sight (*Scaphiopus holbrooki,* Bragg, 1944); enlarged girth and firmness of body (*Rana pipiens* and others, Noble and Aronson, 1942); and differences in kind and amount of activity (*Scaphiopus,* Bragg, 1944; *Staurois,* Liu, 1950; *Bufo,* Savage, 1934; Liu, 1931; Locher, 1939; *Rana,* Banta, 1914) are all felt to be of importance in different species. Visual and olfactory senses have been experimentally approached and discounted for *Xenopus* (Berk *et al.,* 1936; Shapiro, 1937; see also Miller, 1909), while experimental work emphasizes the importance of girth and silence in *Rana* (Noble and Aronson, 1942), and Aronson (1944) has demonstrated the importance of warning vibration in *Bufo.* Noble and Farris (1929) discard Banta's suggestion (1914) of the importance of chemical sense in *Rana sylvatica* and have demonstrated experimentally the importance of girth in the same species. The voiceless *Ascaphus* male is able to recognize the sex

of the clasped individual whether or not the individual struggles (Noble and Putnam, 1931). It seems that different species use different means of sex recognition and that more than one factor is involved. Much of the experimental work since 1930 has been accomplished by injecting the frogs with pituitary extracts. This method is valuable, but there is a question of whether frogs subjected to above-normal dosages of pituitary extract behave as those same individuals would under natural conditions. Rugh (1935) pointed out that male *Bufo fowleri* after receiving pituitary injections will not respond to either the calls or activity of a clasped male, whereas male *Rana* retain their sex recognition abilities under these conditions. The utilization of both field observations and laboratory studies is essential for accurate evaluation of either technique.

Pre-amplectic courtship is one of the more difficult aspects of natural behavior to observe, and it is almost impossible to simulate natural conditions in the laboratory sufficiently to demonstrate its presence. Male *Ascaphus* seek out the female. Male *Scaphiopus holbrooki, Scutiger schmidti, Rana pipiens,* and *Rana nigromaculata* will call until the female approaches and then pursue her, while other *Scaphiopus* will pursue the female as soon as sighted. The male *Syrrhophus* stimulates the female by use of his legs. *Microhyla* and some *Scaphiopus* males will call until touched by the female, while at least in some *Hyla* the female must almost attack the male. *Dendrobates* has carried this further and moves about calling while the female pursues him.

There is a tendency for amplexus to be in the pelvic region in what are generally considered lower forms (*Bombina, Xenopus, Scaphiopus,* and *Scutiger*) and in the pectoral region in the higher forms. *Ascaphus, Alytes,* and *Pipa* have modified their amplexus to adjust to other mating factors (oviposition and care of eggs). Pelvic, pelvo-abdominal, axillary, supra-axillary, supra-pectoral-brachial, neck, inguinal, pectoral, axillo-inguinal, lumbo-pubic, lumbar, and cephalic clasping have been described. The relative size of the mating pair produces considerable variation within species and is perhaps responsible for many differences between related species.

There are several factors that contribute to post-amplectic courting. The backwalking of *Rana pipiens,* the leg movement of *Syrrhophus marnocki,* the toe-thumping of *Bufo nayaritensis,* the wanderings of the female (e.g., stone-hopping in *Staurois*) may all contribute to the completion of proper egg deposition. Further studies may indicate the significance of the calling of males during amplexus and the general restlessness of the females of many species just before oviposition.

All of the complex, and perhaps more or less reflex, movements that tend to bring the cloacas together at the instant of the release of the eggs contribute to the courtship of the mated pair. During amplexus the *Hyla* female flexes her back first, followed by the male; while in *Rana, Staurois, Microhyla,* and *Rhacophorus* the male flexes first. In *Bufo* only the female flexes, but this may be due to the relatively small size of the male. *Ascaphus* has an intromittent organ that assists in fertilization of the eggs. *Alytes* utilizes a cranial amplexus as an aid to fertilization, deposition, and attachment of the eggs to the hind legs of the male. A very complex mating process has been developed in *Pipa* in connection with the ovipositor and dorsal brood pouches of the female. Of additional interest are the African bufonids (*Nectophrynoides*) which are ovoviviparous, but the method of mating is at present unknown (Orton, 1951). Some modifications in courtship and mating behavior are to be expected in *Leiopelma,* which has direct development, and in *Rhinoderma.*

The release after oviposition of the female by the male has been described in several species, but details of the mechanisms involved are generally lacking. The reduction of girth of the female has been given for *Rana sylvatica* (Noble and Far-

ris, 1929), while Noble and Aronson (1942) suggest for other *Rana* a combination of the number of ejaculations of the male, the reduction of girth in the female, and cessation of female amplectic reflexes, including the abandonment of the oviposition posture. A "backflip" by the female is used in *Hyla* (Aronson, 1943*a*), while a "backarch" is used by *Bufo* (Aronson, 1944; Liu, 1931) and a stretching by *Rana planeyi* (Liu, 1930). A characteristic call is apparently involved in the release mechanism in *Phyllomedusa* (Lutz, 1947), while *Microhyla* females obtain their release by leaving the water.

Of immediate value may be the use of courtship patterns as an indication of species affinities. The minor differences between the several *Rana, Bufo,* and *Scaphiopus* species are probably not important in the study of over-all evolutionary trends but they are quite likely important as isolating mechanisms which maintain species integrity where closely related species overlap. The importance, in this respect, of the conditions that initiate breeding (Blair, 1942, 1952; Bragg, 1941, 1944), the place of calling (Bragg, 1940), the call itself (Blair, 1942, 1947; Lindsey, 1954), and the various amplectic phenomena presented here are all apparent. Storm (1952) has shown that male *Rana aurora* will clasp small female *Rana catesbeiana* for a considerable time (four days). This may indicate that isolating mechanisms have not developed between these normally widely separated species or, since fertile eggs were not produced, it may suggest a lack of the proper amplectic stimulus-release responses.

The forms studied are too few, the studies too deficient in detail; the gross and important gaps in our knowledge of *Leiopelma* and *Rhinoderma* prevent the tracing of a complete phylogenetic sequence of courtship and mating behavior from primitive to specialized families, similar to that presented by Noble (1925*a*) for salamanders. In another paper Noble (1925*b*) suggested certain relationships among salientian families but not all of his ideas have withstood the test of time. All the species necessary for the construction of clear-cut family phylogenies may not exist today. The data we have indicate that specializations in mating behavior, mostly revolving around the care of the eggs, are the rule. These vary from mere laying of eggs in protected places, through complex aquatic, terrestrial, and arboreal nesting habits, and ultimately to direct development and ovoviviparity. These developmental trends occur independently of phyletic lines and are believed to represent a general evolutionary tendency of the Salientia. Similar tendencies may be indicated in the courtship patterns. Directly correlated with the tendency for direct development of the embryo is the transfer of much or all of the mating behavior from the aquatic to the terrestrial situation. The movement of amplexus from pelvic to pectoral regions, thus bringing the cloacas together, has been developed independently in some members of several of the so-called primitive families, as well as all of the higher families. There also appears a tendency for the female to play an ever-increasing role in the courtship pattern, becoming a more and more active participant.

Despite the gaps in the record these tendencies are worthy of speculation. They are presented here with the firm belief and hope that they will be replaced by more accurate concepts. If they serve as a stimulus for more work they will have served a useful purpose.

Summary

Accounts of the courtship and mating patterns of several Salientia have been brought together in an attempt to reveal major gaps in the record, evolutionary tendencies, and generalities of behavior.

A wide variety of factors may contribute to, or be necessary for, the initiation of successful reproduction. The calls were found to be a very important part of the mating process, used to establish home

sites, attract the female to the breeding site, stimulate the female before and during amplexus, and to provide a means of sex recognition.

Several frogs (*Rhinophrynus, Scutiger, Scaphiopus, Xenopus, Bombina, Pipa,* and *Ascaphus*) were found to be alike in having pelvic or modified pelvic amplexus. *Pipa* and *Ascaphus* have developed specializations in coupling to adjust for the presence of an ovipositor in the first, and an intromittent organ in the second. Most of the other groups are similar in having a pectoral-type amplexus. Among the latter, various modifications have occurred to bring the cloacas together during spawning. In *Bufo,* only the female flexes during amplexus, while in *Hyla* the female flexes first followed by the male's flexing. The *Microhyla, Rana, Staurois,* and *Rhacophorus* male flexes first, followed by the female. The deposition of the eggs into a triangular area formed by the legs emphasizes the relations between *Rana* and *Staurois.*

A general tendency for mating and development to be transferred from aquatic (*Xenopus, Bufo*) to terrestrial (*Alytes*) and arboreal (*Phyllomedusa*) situations or to the carrying of the embryos by the parents (*Pipa, Rhinoderma*) is indicated. There also appears to be a tendency for the female to play an ever-increasing role in the courtship pattern, being a passive member in *Ascaphus* and the active pursuer in *Dendrobates.*

Intermediate conditions exist in *Rana* and *Scaphiopus,* where the male calls until the female approaches and then pursues her, and in *Microhyla,* where the male calls until touched by the female. The available information was found to be too incomplete to permit the construction of a clear-cut phylogenetic sequence of courtship and mating behavior.

LITERATURE CITED

Anderson, P. K. 1954. Studies in the ecology of the narrow-mouthed frog *Microhyla carolinensis carolinensis. Tulane Studies Zool.,* 2(2):15–46.

Archey, G. 1922. The habitat and life history of *Liopelma hochstetteri. Rec. Canterbury Mus.,* 2:59–71.

Aronson, L. R. 1943*a*. The sexual behavior of anura. 3. The "release mechanism" and sex recognition in *Hyla andersonii. Copeia,* (4):246–249.

——— 1943*b*. The sexual behavior of anura. 4. Oviposition in the mink frog, *Rana septentrionalis* Baird. *Amer. Midl. Nat.,* 29:242–244.

——— 1943*c*. The sexual behavior of anura. 5. Oviposition in the green frog *Rana clamitans,* and the bull frog *Rana catesbeiana. Amer. Mus. Novitates,* No. 1224:1–6.

——— 1944. The sexual behavior of anura. 6. The mating pattern of *Bufo americanus, Bufo fowleri,* and *Bufo terrestris. Amer. Mus. Novitates,* No. 1250:1–15.

Aronson, L. R., and Noble, G. K. 1945. The sexual behavior of anura. 2. Neural mechanisms controlling mating in the male leopard frog, *Rana pipiens. Bull. Amer. Mus. Nat. Hist., 86*:85–139.

Banta, A. M. 1914. Sex recognition and the mating behavior of the wood frog, *Rana sylvatica. Biol. Bull., 26*:171–183.

Barbour, R. W., and Walters, E. P. 1941. Notes on the breeding habits of *Pseudacris brachyphona. Copeia,* (2):116.

Bartlett, A. D. 1896. On the breeding of *Pipa americana. Proc. Zool. Soc. London,* pp. 595–597.

Berk, L. 1938. Studies in the reproduction of *Xenopus laevis.* 1. The relation of external environmental factors to the sexual cycle. *S. Afr. Jour. Med. Sci., 3*:72–77.

Berk, L., Cheetham, R. W. S., and Shapiro, H. A. 1936. The biological basis of sexual behavior in Amphibia. 3. The role of distance receptors in the establishment of the mating reflex (coupling) in *Xenopus laevis* (the South African clawed toad): the eyes. *Jour. Exp. Biol., 13*:60–62.

Blair, A. P. 1942. Isolating mechanisms in a complex of four species of toads. *Biol. Symp., 6*:235–249.

——— 1947. Field observations on spadefoot toads. *Copeia,* (1):67.

——— 1952. Notes on amphibians from Oklahoma and North Dakota. *Copeia,* (2):114–115.

Blair, W. F., and Pettus, D. 1954. The mating call and its significance in the Colorado River toad (*Bufo alvarius* Girard). *Tex. Jour. Sci., 6*:72–77.

Bles, E. J. 1905. The life history of *Xenopus laevis* Daud. *Trans. Roy. Soc. Edinburgh, 41*:789–821.

Bogert, C. M. 1947. A field study of homing in the Carolina toad. *Amer. Mus. Novitates,* No. 1355:1–24.

BOULENGER, G. A. 1886*a*. Remarks in connection with the preceding note. *Annals Mag. Nat. Hist., 17*:463–464.

——— 1886*b*. On the reptiles and batrachians of the Solomon Islands. *Trans. Zool. Soc. London, 12*:35–61.

——— 1896–97. The tailless batrachians of Europe. Ray Society, London. iii + 376 pp. (2 vols.)

——— 1912. Some remarks on the habits of British frogs and toads. *Proc. Zool. Soc. London, 1*:19–22.

BRAGG, A. N. 1937. Observations on *Bufo cognatus* with special reference to breeding habits and eggs. *Amer. Midl. Nat., 18*:273–284.

——— 1940*a*. Observations on the ecology and natural history of anura, I. Habits, habitat, and breeding of *Bufo cognatus*. *Soc. Amer. Nat., 74*:322–349; 424–438.

——— 1940*b*. Observations on the ecology and natural history of anura, II. Habits, habitat, and breeding of *Bufo woodhousii woodhousii* (Girard) in Oklahoma. *Amer. Midl. Nat., 24*:306–321.

——— 1941. Observations on the ecology and natural history of anura, VIII. Some factors in the initiation of breeding behavior in anura. *Turtox News, 19*:10–12.

——— 1944. Observations on the ecology and natural history of anura, XII. The spadefoot toads in Oklahoma with a summary of our knowledge of the group, I. *Amer. Nat., 78*:517–533.

——— 1945. Observations on the ecology and natural history of anura, XII. The spadefoot toads in Oklahoma with a summary of our knowledge of the group, II. *Amer. Nat., 79*:52–57.

CARR, A. F. 1940. Dates of frog choruses in Florida. *Copeia*, (1):55.

COURTIS, S. A. 1907. Response of toads to sound stimuli. *Amer. Nat., 41*:677–682.

CREASER, C., and GORBMAN, A. 1939. Species specificity of the gonadotropic factors in vertebrates. *Quart. Rev. Biol., 14*:311–331.

CUMMINS, H. 1920. The role of voice and coloration in spring migration and sex recognition in frogs. *Jour. Exp. Zool., 39*:325–343.

DE L'ISLE DE DRENEUF, A. 1876. Mémoire sur les moeurs et l'accouchement de l'*Alytes obstetricans*. *Ann. Sc. Nat., 3* (7):1–51.

DUNN, E. R. 1941. Notes on *Dendrobates auratus*. *Copeia*, (2):88–93.

FERMIN, P. 1765. Développement parfait du mystère de la génération du fameux crapaud de surinam. Maestricht, 1765 (abstract).

FIRSCHEIN, I. L. 1951. A peculiar behavior pattern in a Mexican toad, *Bufo nayaritensis*, during amplexus. *Copeia*, (1):73–74.

FLETCHER, J. J. 1889. Observations on the oviposition and habits of certain Australian batrachians. *Proc. Linn. Soc. N. S. Wales* (2), *4*:357–387.

GOELDI, E. A. 1895. Contribution to the knowledge of the breeding habits of some tree frogs (Hylidae) of the Serra dos Orgaos, Rio de Janeiro, Brazil. *Proc. Zool. Soc. London*, pp. 89–97.

GOIN, C. J. 1948. The peep order in peepers; a swamp water serenade. *Quart. Jour. Fla. Acad. Sci., 11*:59–61.

GOLDSCHMIDT, G. W. 1926. Habits and reactions of *Scaphiopus hammondi*. *Yearbook Carnegie Inst. Wash., 25*:369–370.

JAMESON, D. L. 1954. Social patterns in the Leptodactylid frogs *Syrrhophus* and *Eleutherodactylus*. *Copeia*, (1):36–38.

——— (In press.) The population dynamics of the cliff frog, *Syrrhophus marnocki*. *Amer. Midl. Nat.*

——— (In press.) Population structure and homing response in the Pacific tree frog. *Copeia*.

LINDSAY, H. L. 1954. The narrow-mouthed toads *Microhyla olivacea* and *M. carolinensis* in northeastern Oklahoma. *Copeia*, (2): 158.

LITTLEFORD, R. A. 1946. A congress of Fowler's toad. *Copeia*, (2):104.

LIU, C. C. 1930. Secondary sexual characters and sexual behavior in peeping toads and frogs. *Peking Nat. Hist. Bull., 5*:49–52.

——— 1931. Sexual behavior in the Siberian toad, *Bufo raddei* and the pond frog, *Rana nigromaculata*. *Peking Nat. Hist. Bull., 6*: 43–60.

——— 1950. Amphibians of western China. *Fieldiana: Zool. Memoirs, 2*:1–400.

LOCHER, C. J. S. 1939. Over padden. *Pevende Natuur., 44*:129–135.

LUTZ, BERTHA. 1947. Trends toward nonaquatic and direct development in frogs. *Copeia*, (4):242–252.

——— 1948. Ontogenetic evolution in frogs. *Evolution, 2*:29–39.

LYNN, W. G. 1942. The embryology *of Eleutherodactylus nubicola*. *Carnegie Inst. Wash. Contr. Embryology, 190*:27–62.

MARTOF, B. S. 1953. Territoriality in the green frog, *Rana clamitans*. *Ecology, 34*: 165–174.

MAYNARD, E. A. 1934. The aquatic migration of the toad, *Bufo americanus* Le Conte. *Copeia*, (4):174–177.

MILLER, N. 1909. The American toad. *Amer. Nat., 43*:641–668; 730–745.

MULAIK, S. 1937. Notes on *Leptodactylus labialis* (Cope). *Copeia*, (1):72–73.

NOBLE, G. K. 1923. Voice as a factor in the mating of batrachians. *Science, 58*(1501): 270–271.

——— 1925*a*. An outline of the relation of ontogeny to phylogeny within the amphibia, I. *Amer. Mus. Novitates,* No. 165:1–17.

——— 1925*b*. An outline of the relation of ontogeny to phylogeny within the amphibia, II. *Amer. Mus. Novitates,* No. 166:1–10.

——— 1927. The value of life history data in the study of the evolution of the Amphibia. *Annals N. Y. Acad. Sci., 30*:31–128.

——— 1931. The biology of the Amphibia. McGraw-Hill Book Co., Inc., New York. xiii + 577 pp.

NOBLE, G. K., and ARONSON, L. R. 1942. The sexual behavior of anura, 1. The normal mating pattern of *Rana pipiens. Bull. Amer. Mus. Nat. Hist., 80*:127–142.

NOBLE, G. K., and FARRIS, E. J. 1929. The method of sex recognition in the woodfrog, *Rana sylvatica* Le Conte. *Amer. Mus. Novitates,* No. 363:1–17.

NOBLE, G. K., and NOBLE, R. C. 1923. The Anderson tree frog (*Hyla andersonii* Baird). *Zoologica,* New York, *2*:413–455.

NOBLE, G. K., and PUTNAM, P. G. 1931. Observations on the life history of *Ascaphus truei* Stejneger, *Copeia,* (3):97–101.

ORTON, GRACE L. 1943. The tadpole of *Rhinophrynus dorsalis. Occ. Pap. Mus. Zool. Univ. Mich.* No. 472:1–7.

——— 1949. Larval development of *Nectophrynoides tornieri* (Roux), with comments on direct development in frogs. *Annals Carnegie Mus., 31*:257–276.

——— 1951. Direct development in frogs. *Turtox News, 29*:2–6.

——— 1955. Some aspects of ecology and ontogeny in the fishes and amphibians. *Amer. Nat., 89*:193–203.

POPE, C. H. 1931. Notes on amphibians from Fukein, Hainan, and other parts of China. *Bull. Amer. Mus. Nat. Hist., 61*:397–611.

RUGH, R. 1935. Pituitary-induced sexual reactions in the anura. *Biol. Bull., 68*:74–81.

——— 1937. A quantitative analysis of the pituitary-ovulation relation in the frog (*Rana pipiens*). *Physiol. Zool., 10*:84–100.

——— 1948. Experimental embryology. Burgess Publ. Co., Minneapolis, vii + 481 pp.

SAMPSON, LILLIAN V. 1900. Unusual modes of breeding and development among anura. *Amer. Nat., 34*:687–715.

SAVAGE, R. W. 1934. The breeding behavior of the common frog *Rana temporaria* and of the common toad *Bufo bufo. Proc. Zool. Soc. London,* (1):55–70.

——— 1935. The influence of external factors on the spawning date and migration of the common frog, *Rana temporaria. Proc. Zool. Soc. London,* (1):49–98.

SHAPIRO, H. A. 1936*a*. The biological basis of sexual behavior in amphibia, I. The experimental induction of the mating reflex (coupling) in *Xenopus laevis* (the South African clawed toad) by means of pregnancy urine and of anterior pituitary extracts, with the production of fertilized ova. *Jour. Exp. Biol., 13*:48–56.

——— 1936*b*. The biological basis of sexual behavior in amphibia, II. The independence of ovulation and coupling (the mating reflex) in *Xenopus laevis* (the South African clawed toad). *Jour. Exp. Biol., 13*:57–59.

——— 1937. The role of distance receptors in the establishment of the mating reflex in *Xenopus laevis:* the nares. *Jour. Exp. Biol., 14*:38–47.

SLATER, J. R. 1931. The mating behavior of *Ascaphus truei* Stejneger. *Copeia,* (2):62–63.

SMITH, R. E. 1940. Mating and oviposition in the Pacific coast tree toad. *Science, 92* (2391):379–380.

STORM, R. M. 1952. Interspecific mating behavior in *Rana aurora* and *Rana catesbeiana. Herpetologica, 8*:108.

STUART, L. C. 1935. A contribution to a knowledge of the savanna region of central Peten, Guatemala. *Misc. Publ. Univ. Mich. Mus. Zool., 29*:1–59.

WRIGHT, A. H. 1914. North American anura. Life histories of the anura of Ithaca, New York. *Carnegie Inst. Wash. Publ.,* No. 197. viii + 98 pp.

YERKES, R. M. 1905. The sense of hearing in frogs. *Jour. Comp. Neur. Psych. 15*:279–304.

D. L. JAMESON is Assistant Professor of Biology, University of Oregon, Eugene, Oregon. The writer wishes to thank W. F. Blair, G. L. Orton, and C. M. Bogert for reading the manuscript.

An Interpretation of the Structure and Distribution of Cnidae in Anthozoa

CHARLES E. CUTRESS

DURING the past century many publications on coelenterate cnidae (nematocysts) have appeared, but, apart from the major paper of Weill (1934) and two of Carlgren (1940 and 1945), they do not have direct bearing on this study or are only of historical interest. An excellent review of the literature previous to 1934 can be found in Weill's monograph. In this treatise on the cnidae Weill has associated the nematocyst types of earlier authors with the categories of his own system of classification. In his scheme of nomenclature the cnidae are divided into the two general groups, nematocysts and spirocysts. The spirocysts are not subdivided, being retained by Weill as a category which closely follows the definition of Bedot (1896). The nematocysts, on the other hand, he divided into astomocnides and stomocnides. In turn, the stomocnides are divided into haplonemes, heteronemes, and rhopaloides. The haplonemes and heteronemes (only stomocnides occurring in the Anthozoa) he arranged in a succession of smaller and more specific units. The definitive appellatives of these two groups—basitrichs, microbasic mastigophores, micro- and macrobasic amastigophores, holotrichs and atrichs—along with the spirocysts, are those that subsequently have been used to refer to Anthozoan cnidae. Carlgren (1940) subdivided Weill's microbasic mastigophores into macrobasic *b*-mastigophores and microbasic *p*-mastigophores. The nomenclature of Weill, as modified by Carlgren, is used in this paper with the exception that it is proposed to eliminate two categories (microbasic and macrobasic amastigophores) and to add two new ones (microbasic *q*-mastigophores and macrobasic *p*-mastigophores).

The nomenclature of the categories of cnidae is not so much the concern of this paper as are the finer diagnostic structures. The current nomenclature is descriptive and, with the exceptions of the amastigophores, microbasic *q*-mastigophores, and macrobasic *p*-mastigophores, sufficient. With the same exceptions, the definitions of the categories are detailed and accurate. It is only the association of many of the nematocysts with the definitions that is in error, the errors being the result of misinterpretation of the fine structure of the nematocysts. For example, the long, thin cnidae with completely coiled capsular content that are so characteristic of the marginal spherules (acrorhagia) are commonly considered by actinologists to be atrichs, and only when the armature of the tube is very coarse do they recognize them as holotrichs. Actually, armature is always present on the tube but sometimes is very fine and care must be taken to resolve it under the microscope.

A somewhat different case is that of a nematocyst type, characteristic of the Boloceroididae, which usually is referred to the microbasic amastigophores. Here even a careful examination of the ends of the shafts of many of these nematocysts, when they are exploded in fresh preparations, does indeed indicate that they are amastigophoric (lacking a thread). However, if observations are extended to the

unexploded nematocysts and if the process of uncoiling in this particular type is carefully followed, an entirely different picture emerges. These nematocysts characteristically have a very thin thread which forms a loop between the notch at the end of the shaft and the blind end of the capsule to which the distal end of the thread apparently adheres. Upon evagination of the capsular content, the thread usually breaks at the point of attachment with the shaft and remains in the capsule. However, it occasionally evaginates with the shaft. In any case, these nematocysts do possess a thread and should be classed as microbasic *p*-mastigophores, not microbasic amastigophores.

If the cnidae are to have value in systematics they must be susceptible of consistent and reasonably rapid identification. This is possible only when the absolute diagnostic characteristics of the cnidae have been determined. Ideally these characters should be distinguishable either in the intact or exploded state. Thus, through re-evaluation of the present categories of nematocysts (based on new interpretations of their finer structures) it becomes possible to associate the nematocysts more precisely with the existing definitions.

No attempt is made in this paper to go into the complete structure of the cnidae or to point out all the confusion in previous publications. Only those aspects of the cnidae which appear to be useful in systematics are covered. Most of the data used in the preparation of this paper were obtained from examination of unpreserved material. All of the major groups of the Anthozoa have been examined, except the tribus Protantheae and order Ptychodactiaria, but the cnidae described and figured for these groups by other investigators have been readily recognized and are considered. Most of the figures of capsules are drawn to scale but the tube and armature are not. The details of the figures are accurate with the exception that only one of the three bands of armature has been drawn on the tubes. The capsule sizes are referred to only when pertinent to the discussion.

General Considerations

The cnidae are the intricate, non-living products of certain apparently undifferentiated coelenterate cells. It is not known whether one cell is capable of producing more than one nematocyst or more than one kind of nematocyst. During the early stages of cnidogenesis the types of nematocysts contained within the secreting cells are almost indistinguishable one from the other. It is only during the later stages that the great variety of form and size of the nematocysts becomes apparent. It is these cnidae of variable size and structure which, when evaluated and classified, lend themselves so well to systematics.

The size of the capsule was probably the first feature of the cnidae used in classification of species of coelenterates. Many investigators who make no attempt to give the cnidom for a species will list sizes of the more conspicuous categories of cnidae. Carlgren (1900), referring to Actiniaria, pointed out that "no description of a species is complete unless it includes notes on the size of the nematocysts." However, neither size of nematocysts for the larger taxonomic groups nor randomly selected measurements of nematocysts from a species are necessarily of taxonomic value. To be diagnostic the measurements of nematocysts must be taken from all the major kinds that comprise the cnidom of the species. Frequently, obviously aberrant dwarfs or giants appear in all the categories, but they are of no importance to the diagnosis. Equally as important as knowing the sizes of all the categories of nematocysts is the knowledge of which specific organs or parts of organs were the source of the measured nematocysts. For example, in *Rhodactis* sp. macrobasic *p*-mastigophores (in this case the holotrichs of Weill and

Carlgren) from the distal parts of the filaments are more than twice the size of those from the proximal parts of the filaments. Also essential is the knowledge of degree of maturity of the animal from which the nematocysts are examined. Young animals frequently possess categories of nematocysts that are absent in adults, and also the sizes of those kinds that are present in both often differ markedly.

The nomenclature of Weill and Carlgren is based solely on the capsular content, but in specific instances the shape of the capsule has utility in the scheme of classification. The capsule, in silhouette, may have the shape of a straight rod, a bent rod, a bottle; it may be lenticular, pyriform, ovoid, spherical, or any variation of these forms. Sometimes the shape of the capsule is very distinctive, e.g., the bottle-shaped microbasic *b*-mastigophores of some species of *Actinothöe*. This feature alone may not be significant in the total cnidom of the genus but coincident with other characteristics it is of great help in recognizing the species.

A trivial detail but one related to capsular structure is the "operculum." Weill (1934) is the only recent author to make a point of it but he does not make clear what he means by the term. He draws it (p. 23, Fig. 10*a*) as a cap over the aperture of the undischarged nematocyst, but if this were true it could not possibly persist in the discharged state as he has drawn it (p. 23, Fig. 10*b*). If he implies there is a cap over the aperture, he is in error, and if he means there is a thickened rim or flange around the aperture, his choice of the term, operculum, is misleading. I have never seen evidence of an operculum on an anthozoan nematocyst. If there were an operculum (cap) present, the tip of the shaft would not protrude beyond the aperture of the capsule as it commonly does in certain kinds of nematocysts (Fig. 1, *f*). All evidence suggests that the aperture is surrounded by a thickened ridge or flange at the juncture of the capsule wall with the tube (Fig. 1, *f,g*).

The capsular content exhibits by far the greatest variation of form, and for this reason the nomenclature is based on it. In a limited sense the capsular content is the tube. Granules and fluids contained in the capsule with the tube bear little significance to this study. The tube of the nematocyst may be short or long and may be, with respect to diameter, undifferentiated or divisible into a portion of greater diameter (the shaft) and a portion of lesser diameter (the thread). The tube may be smooth (?) or bear three helically-coiled bands of armature which may extend throughout its length or be restricted to some fraction thereof. The armature, in turn, may vary from very long and coarse to nearly imperceptible spines. The armature varies in length on different regions of the tube of a single nematocyst as well as between categories of cnidae. The presence of armature on the tube is so characteristic for most nematocysts (I have found it throughout the length of all types of tubes except the terminal portion of basitrichs and the entire tube of atrichs) that it may very well be that all nematocyst tubes are or have been armoured throughout their length. It seems that some atrichs in the Ceriantharia and Corallimorpharia may very well be macrobasic *p*-mastigophores which have lost their armature. The structure of the tube and its armature is more fully covered in the discussion of the categories of cnidae.

There are two opposing opinions on the inherent character of the undischarged tubes of nematocysts which have a distinct shaft, but both are somewhat vague as to details. It may, therefore, be advantageous at this time to explain the configuration of these tubes. Moebius (1866), Bedot (1886), and Gosse (1860), in particular, have indicated that, in those nematocysts with a shaft of considerably greater diameter than the thread, the shaft is folded within itself (Fig. 1, *a*). If

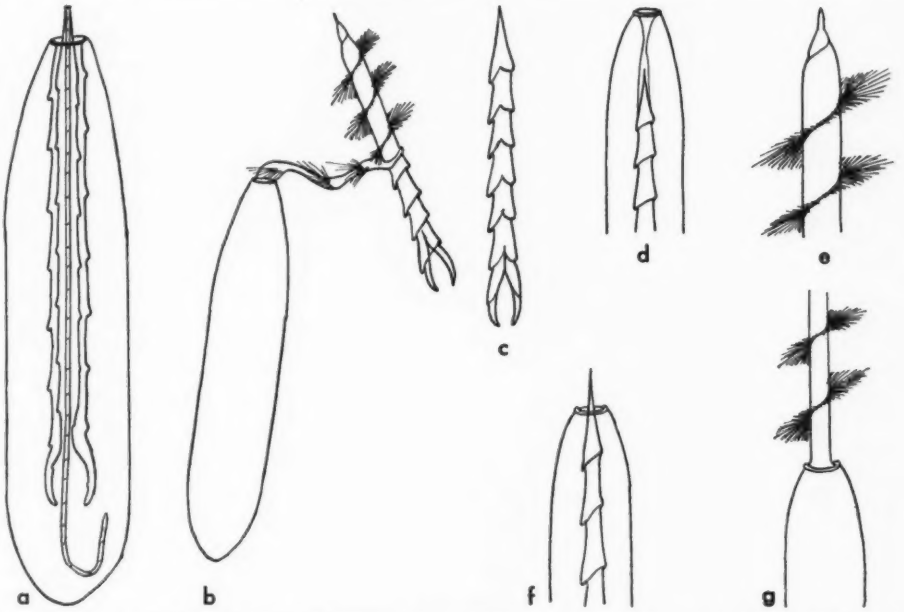

FIG. 1. Microbasic *p*-mastigophores. (*a*) diagram of invaginated and folded shaft with thread; (*b*) crushed specimen with proximal shaft wall torn away exposing infolded distal part of shaft; (*c*) isolated, invaginated shaft showing angle of folded armature is several times greater than angles of the shaft's point and notch; (*d*) proximal portion of invaginated shaft between the capsule aperture and point of the shaft; (*e*) example of a vestigial thread; (*f*) point of shaft protruding beyond the capsule aperture; also, showing flange (rim) around aperture; (*g*) showing persistence of flange after evagination of shaft.

the shaft is thus folded the thread (always present?) will then be attached at the point of the shaft which is usually in the aperture of the capsule. Weill (1934), in describing the type morphology of a nematocyst (microbasic *p*-mastigophore), has rejected the interpretations of these earlier investigators. He (p. 23, Fig. 10*a*) shows the shaft to be inverted but not folded and the thread to be attached to the end of the shaft farthest from the capsule aperture. Figure 1, *b* illustrates a crushed nematocyst in which the shaft, although partly attached, has been forced out through a split in the capsule. In this instance part of the shaft has also split and pulled away, exposing the folded section. Accidentally crushed preparations like Figure 1, *b* conclusively show the shaft to be folded as well as invaginated. Further substantiating evidence is that encountered in some large macrobasic *p*-mastigophores in which the distal end (the point) of the shaft does not reach the aperture of the capsule (Fig. 1, *d*). Here a tube (the base of the shaft) can be seen extending from the aperture, sometimes for a considerable distance, to the point of the shaft.

Weill (1934, p. 23, Fig. 10*a*) shows the point at the aperture end of the undischarged shaft and the notch at the opposite end to be the result of the armature folded within the tube. His figure is without doubt that of a microbasic *p*-mastigophore but is not an accurate depiction. Figure 1, *c* is more nearly the configuration of an isolated, undischarged shaft of a microbasic *p*-mastigophore. In this figure it can be seen that the angles formed

by the folded armature are decidedly less acute than the angles of the notch and point of the shaft. This observation and the fact that the point does not fray out when protruding beyond the aperture indicates rather conclusively that the point and the notch of the tube are not configurations of the armature. There is strong evidence, then, that in those nematocysts with a shaft of considerably greater diameter than the thread the shaft is both invaginated and folded back within itself. This folding of the shaft brings the tip of the shaft (the juncture with the thread) to a position in or near the capsule aperture. The categories of nematocysts exhibiting this phenomenon are micro- and macrobasic *p*-mastigophores and microbasic *q*-mastigophores. All other types of nematocysts have a tube which is simply inverted within the capsule.

The staining reactions exhibited by cnidae suggest that there are chemically different types. The spirocysts, for example, are well known for their affinity for acid dyes, and equally well known is the affinity of the "nematocysts" for basic dyes. There are, however, nematocysts which are completely refractory to both acid and basic dyes. Other evidence suggesting chemically different types of nematocysts is that of the variation in their toxicity. Different categories of cnidae, and even the same morphological types from different species, may produce markedly different toxic reactions in other animals. So little is now known about the chemical nature of nematocysts that attempted use of their chemical characteristics in classification would only be confusing.

All the previously mentioned characteristics of the cnidae mean little in a systematic diagnosis unless the distribution of the cnidae is also given. Considering first the distribution of the cnidae in the organs of Anthozoa, most of the organs of both entodermal and ectodermal origin contain nematocysts. Nematocysts are not an intrinsic feature of the mesoderm. Almost every category of cnidae occurs in both the ectoderm and entoderm in at least some species, but it is doubtful if this can be said of the spirocysts. When spirocysts are described from entodermal organs, such as filaments, they are almost certainly contaminants. Some organs of a species may contain several categories of nematocysts. For example, the marginal spherules (acrorhagia) of *Phymactis clematis* possess holotrichs, microbasic *b*-mastigophores, and spirocysts. On the other hand, an organ may contain no nematocysts (the ectoderm of the column of some Alcyonaria) or only one kind (microbasic *p*-mastigophores in the acontia of *Sagartiomorphe*). In deriving the cnidom for a species it is thus most important to consider the types of nematocysts for all organs of the animal. When the cnidom is well known for all species of a genus or family, it is frequently found that the distribution, together with morphological characteristics, of the cnidae is also diagnostic for the genus or family. As an example, I re-cite the situation of the peculiar microbasic *p*-mastigophores found in all species of the family Boloceroididae. On the basis of morphological characteristics, Carlgren (1924) assembled the genera, *Boloceroides* and *Bunodeopsis*, into the family Boloceroididae. Now we have the additional evidence of a carefully determined cnidom which substantiates his phylogenetic arrangement.

Carlgren (1945, pp. 21–23) gives a survey of the distribution of the categories of cnidae for most anthozoan genera. However, it must be remembered that some of the categories of nematocysts in this survey have been confused one with the other, and all will ultimately have to be reinterpreted.

Spirocysts, Bedot 1890

The spirocysts, because of their apparent differences from other nematocysts, have usually been considered a group apart from them. Weill (1934) devoted three short chapters to the spirocysts. He has chiefly summarized the

older works on the spirocysts, adding very little new knowledge. As a result, our information on this group is little more than that given in the usual definition for it. Generally, the spirocysts are characterized as having affinity for acid dyes, and as having a thin, single-walled capsule and an unattached, solid, smooth, coiled thread which, when released from the capsule, unravels rather than evaginates. However, the examination of many spirocysts from many species brings to light discrepancies in the preceding definition. It is agreed that most spirocysts do have an affinity for acid dyes but at the same time there are some with a more or less neutral reaction to them. With respect to the structure of spirocysts I am in disagreement with almost all earlier interpretations except those of Will (1909) who is of the opinion that spirocysts are essentially the same as nematocysts.

The capsule walls of spirocysts exhibit every degree of thickness and refringence that can be found in the capsule walls of nematocysts. The development of the spirocysts in the cnidoblasts is, to my knowledge, much the same as for holotrichs, for example, and there is no reason to believe the capsule is single-walled in one case and double-walled in the other. Being a secreted structure the spirocyst is probably laid down in much the same way as the cuticular surface of certain epithelia. The capsule walls of spirocysts are usually very thin in actiniarians (Fig. 2, *a–e*) but generally thick in the corallimorpharians and ceriantharians (Fig. 2, *f–j*).

The distinction that the thread of the

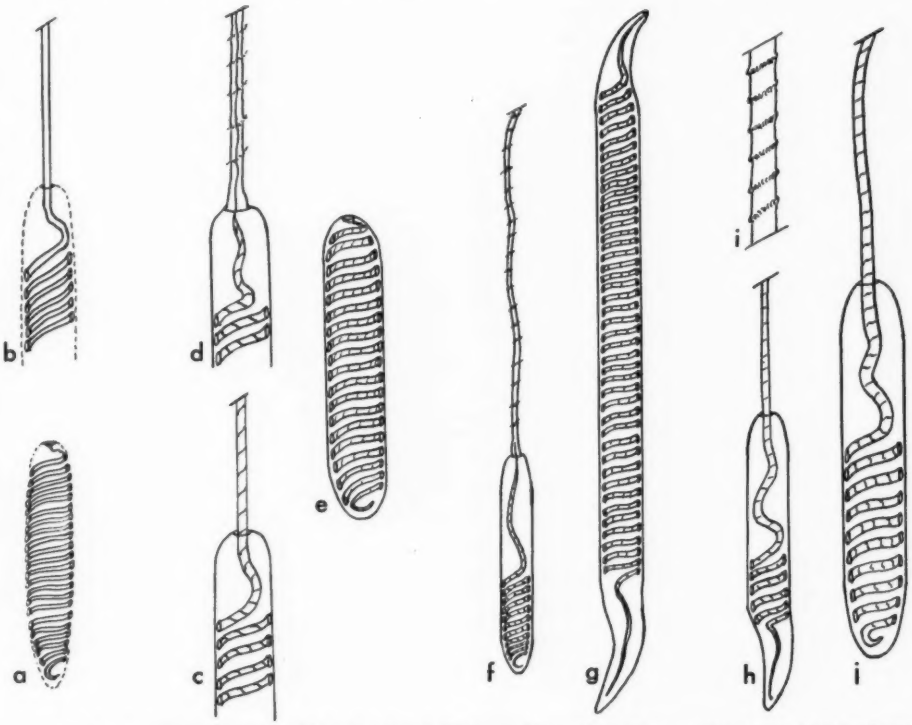

FIG. 2. Spirocysts. (*a,b*) *Aiptasia;* (*c–e*) *Boloceroides;* (*f,g*) *Corynactis;* (*h–j*) *Cerianthus;* (*i*) portion of invaginated tube, *Cerianthus.*

spirocyst is unattached and unravels is only partly true. When carefully made preparations are examined, the tubes of many spirocysts can be seen to be weakly attached to the capsules. This attachment is more readily observed when the preparations are from very young animals. In those spirocysts in which the tube is attached, the wall of the tube is considerably thinner at its juncture with the capsule wall and is usually deflated, wrinkled and twisted. When the tube remains attached there is enough purchase for the tube to evaginate precisely as it does in other nematocysts (Fig. 2, *d,f*). On the other hand, when the tube becomes detached, it unravels in an inverted condition (Fig. 2, *b,c,h,j*). The fact that the tube evaginates on occasion proves beyond doubt it is a tube and not a solid thread. In addition, drops of acid fuchsin in the lumens of both unraveled and evaginated tubes will occasionally traverse their lengths and spill out at the ends. The tubes of all spirocysts examined bore armature or evidence of armature. Very likely the reason other investigators have considered the tubes of spirocysts smooth is that the armature is sometimes fine, and because the tube only rarely evaginates, usually is found on the inside of the tube. However, the armature of most spirocyst tubes is no finer than that on the tube of the average holotrich, and with good resolution it can be discerned in either the unraveled or evaginated state. When the armature is on the inside of the tube it causes periodic, tangential ridges on the outer side of the tube.

Because the capsular contents of the spirocysts are quite uniform in structure, only the variability of the capsule size and shape and the distribution of the spirocysts in the species are of importance in systematics. Figure 2 illustrates a few shapes and sizes of spirocyst capsules. The spirocysts are probably restricted to the ectoderm, being most numerous in the tentacles and diminishing in number toward the mouth and pedal disc. Spirocysts rarely occur in the pedal disc, and some orders contain species which lack them in the column. Among the Anthozoa, spirocysts occur at least sparingly in all the orders except Octocorallia.

In light of these facts, the spirocysts, in all probability, represent a type of nematocyst whose main difference is its chemical nature.

Basitrichs, Weill 1930

The basitrichs are defined by Weill as those nematocysts which have a tube of the same diameter throughout its length and bearing armature on its proximal portion to an extent not exceeding three times the length of the capsule. However, if the characteristics given in the definition are rigidly adhered to, the nematocysts considered by Weill to be basitrichs do not qualify. Almost without exception Weill's basitrichs have a tube which is more rigid at the base, having thicker walls or a greater diameter in that region. All evidence indicates that the base of the tube is of greater caliber than the distal portion. It may be presumptuous to state that the man who defined almost the entire system of cnidae classification failed to recognize his own categories, but this appears to be the case. If Weill's basitrichs are retained as defined there remains a type of cnidae having a general distribution among the Anthozoa that he has failed to consider in its proper perspective. These nematocysts are characterized by having, in the undischarged condition, a completely or almost completely coiled tube which bears armature at the base. The fact that the tube is more or less completely coiled indicates that the proximal part has the same rigidity as the distal portion. This complete coiling results from the tube's being of uniform diameter and/or having walls of uniform thickness. Examples of this type of cnidae are illustrated in Figure 3. The complete coiling of the tube within the capsule and the small size

of these nematocysts distinguish them from all others. Before deciding what to do with this category of nematocysts it would clarify the predicament if the next group to be considered (the microbasic *b*-mastigophores) were briefly previewed. The microbasic *b*-mastigophores are distinguished from the basitrichs by having a tube in which the caliber of the proximal part is slightly greater than that of the distal portion. Now, since there are two adequate categories extant (basitrichs and microbasic *b*-mastigophores) it appears that all that need be done is to restrict the types of nematocysts concerned to the existing definitions and terminologies that best fit them. In the case of the category, basitrichs, I propose to include only those nematocysts (Fig. 3, *a–i*) having completely coiled tubes (therefore of uniform diameter) in the undischarged state and bearing armature at least on their proximal portions. The capsules of these nematocysts rarely attain a length of 40μ.

Failure to recognize the category of nematocysts hereafter referred to as basitrichs has resulted in their being called sometimes atrichs and, at other times, microbasic *b*-mastigophores. For example, the Octocorallia are said to possess a solitary category of nematocysts, the atrichs. In reality the nematocysts of this order are basitrichs. Figure 9, *g,h,i* illustrates a basitrich from *Sarcothelia edmondsoni* Verrill. In addition to the confusion of basitrichs with atrichs, Carlgren has confused the basitrichs with microbasic *b*-mastigophores. He has stated repeatedly that to separate basitrichs from microbasic *b*'s it is necessary to observe them discharged. It is by this reasoning that the confusion exists, for it is next to impossible to determine (with an optical microscope) a difference in diameters of tubes when that difference may be 0.1μ or less. The measurements are further complicated by the diffusion effect of coarse armature at the base of the tube. As already mentioned the basitrichs (as redefined) are more readily distinguished from the microbasic *b*'s when undischarged. The tube of the basitrich is completely coiled in the capsule, whereas in the microbasic *b*'s the basal portion of the tube, because it has a greater diameter, is uncoiled. Some of the basitrichs (Fig. 3, *f*) show a tendency to intergrade with

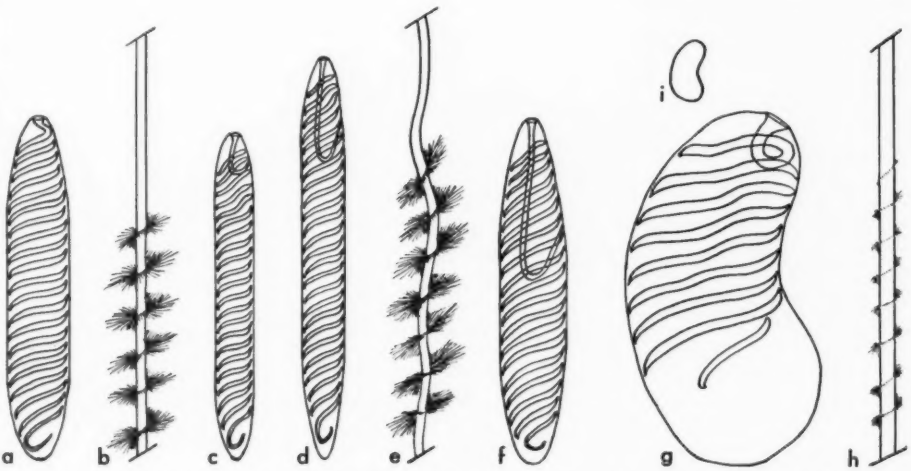

FIG. 3. Basitrichs. (*a,b*) *Anthopleura;* (*c*) *Bunodeopsis;* (*d,e*) *Aiptasia;* (*f*) *Fungia;* (*g–i*) *Sarcothelia;* (*i*) size of "*g*" drawn to scale of other nematocysts in figure.

the microbasic *b*-mastigophores but they are usually few in number and not critical to the diagnosis.

In distribution the basitrichs are more numerous in the tentacles, oral disc, and column. In the Actiniaria they are usually an inconspicuous category, being rare or absent in many genera. In the Octocorallia, on the other hand, they are numerous and the only category present.

Microbasic b-*mastigophores, Carlgren 1940*

The microbasic *b*-mastigophores of Carlgren are in part the microbasic mastigophores of Weill. By Weill's definition the tube of the microbasic mastigophore is differentiated into a proximal, armoured shaft less than three times the length of the capsule and a distal thread which may or may not be armoured (hoplotelic). However, Weill failed to notice that within this category there are nematocysts with two rather different shafts. One type has a shaft that tapers gradually to a thread, the other a shaft that narrows abruptly to a thread. Carlgren (1940) recognized the difference, and, to the type with a gradually tapering shaft he assigned the name, microbasic *b*-mastigophore. Those with abruptly tapering shafts he called microbasic *p*-mastigophores. In short, the microbasic *b*'s have been defined as having a capsular content consisting of an armoured shaft which is less than three times the capsule length and which tapers gradually to a thread that may or may not bear armature (be hoplotelic). Except for the hoplotelic condition of the thread, the definition is adequate for the category of nematocysts depicted in Figure 4. The threads of many nematocysts of this category are certainly hoplotelic. The question is, are the threads of all microbasic *b*'s hoplotelic? Among the microbasic *b*'s from many anthozoan genera examined there were only a few in which armature on the thread could not be resolved. Judging from the general tendency for the nematocysts of this category to be hoplotelic, it seems probable that with greater magnification and resolution they will all be found to have armoured threads. Un-

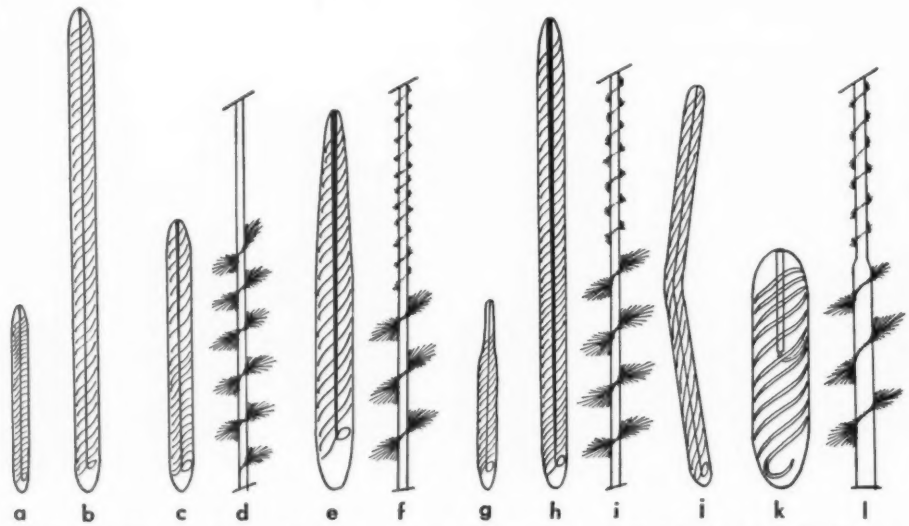

FIG. 4. Microbasic *b*-mastigophores. (*a,b*) *Phymactis;* (*c,d*) *Stoichactis;* (*e,f*) *Pocillopora;* (*g*) *Telmatactis;* (*h,i*) *Edwardsia;* (*j*) *Actiniogcton;* (*k,l*) *Fungia.*

til it can be proved whether or not the thread is always armoured it would seem more expedient for taxonomic purposes to assume all microbasic *b*'s are hoplotelic, or at least to minimize the importance of this feature in the diagnosis.

Like the basitrichs, the microbasic *b*'s are recognized more readily when undischarged. The shaft of the microbasic *b* is more rigid, as a consequence of its greater diameter, than the thread. For this reason the shaft occurs as a straight axial rod of variable length through the center of the capsule. Wherever the shaft may terminate within the capsule, the thread begins to coil around the shaft, against the capsule wall and back toward the capsule aperture.

The capsules of most microbasic *b*'s are quite uniform in shape. They are usually long, thin cylinders (sometimes exceeding 80μ in length), but occasionally are slightly pyriform (Fig. 4, *e*) or bottle-shaped (Fig. 4, *g*). A modification of these capsule shapes, heretofore overlooked, is a very long, thin, bent type which resembles a spicule or piece of straw. It is so thin the capsular content can scarcely be discerned within the capsule, and was never observed to evaginate. One of these nematocysts is illustrated in Figure 4, *j* but is somewhat thicker and shorter than most. They occur in the ectoderm of the column and pedal disc of certain species of Actiniaria. They are most numerous in the pedal disc and become rare toward the margin.

The microbasic *b*-mastigophores, like other categories of nematocysts, are only a segment of a continuous spectrum of nematocyst forms. There are a few microbasic *b*'s (Fig. 4, *k,l*) which intergrade with the microbasic *p*-mastigophores. To repeat, such intergrading forms are not critical in cnidae determinations.

The microbasic *b*-mastigophores seem to be most numerous in the Actiniaria, Zoantharia and Antipatharia; rare in Scleractinia, Corallimorpharia, and Cerianthara; completely lacking in Octocorallia and Ptychodactiaria. The microbasic *b*'s occur in most organs of the animals but usually are most numerous in the tentacles, oral disc, and column. Sometimes they are lacking in organs that usually contain them, for example, the acontia of *Sagartiomorphe*.

Microbasic p-*mastigophores, Carlgren 1940*

The microbasic *p*-mastigophores of Carlgren are those microbasic mastigophores of Weill that have shafts which are abruptly reduced to threads. The shaft has a markedly greater diameter than the thread and, in the inverted condition within the capsule, is folded back within itself, thereby imparting to the folded end the appearance of a cone or V-shaped notch (Fig. 5). The shaft may vary in length from very short (Fig. 5, *b,c*) to three times the length of the capsule, the arbitrary limit for the category. If the undischarged shaft is the length of the capsule, it is almost always approximately twice the capsule length when discharged. The armature of the shaft is usually long and rather coarse,

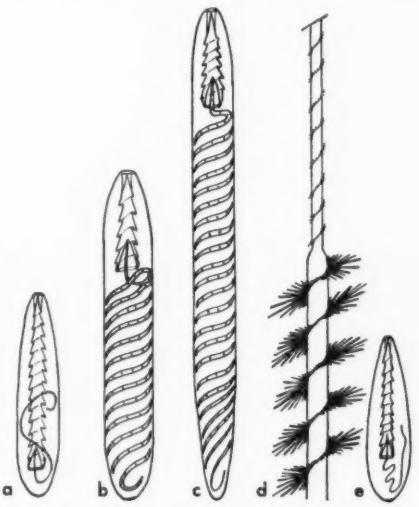

FIG. 5. Microbasic *p*-mastigophores. (*a*) *Anemonia;* (*b*) *Pocillopora;* (*c,d*) *Corynactis;* (*e*) *Cerianthus.*

the bristles sometimes clumping together and obscuring the three helically-coiled bands. The threads of the microbasic *p*'s, like the shafts, are of variable lengths (Fig. 5, *a–c*). Within the capsule the inverted thread, which is attached to the end of the shaft nearest the aperture, passes through the lumen of the shaft, and if the thread is long it coils behind the shaft. The fact that the thread is in the lumen of the shaft does not prohibit its evaginating before the shaft is completely expelled. According to Weill and Carlgren the threads of the nematocysts now called microbasic *p*'s are sometimes hoplotelic, sometimes not, and they have used this characteristic to subdivide the microbasic *p*'s. However, the microbasic *p*'s from numerous species of Anthozoa I have examined were all hoplotelic. The observations seem sufficient to indicate that the threads of all nematocysts of this category may bear armature, but because the presence of armature may sometimes be questionable it has little value in systematics.

Only the structure of the microbasic *p*-mastigophores of Carlgren has been considered. Before going further two other categories of nematocysts should be mentioned, the microbasic amastigophores of Weill and those nematocysts which have an additional discrete, unattached part associated with the capsular content. The latter group has heretofore been included with the microbasic *p*'s but in this paper will be considered a separate category to be described next in order. The amastigophores, according to Weill and Carlgren, have a capsular content consisting of a shaft only which is less than three times the length of the capsule. Carlgren (1945 and 1949) lists thirteen families of Actiniaria which supposedly possess microbasic amastigophores. Representatives of almost every genus of nine of these families were examined, and in every case a thread was found associated with the shaft. There are several reasons why the thread has been overlooked. The most peculiar situation is that of some "amastigophores" in *Bunodeopsis* (Fig. 6, *c,d*), similar kinds of which also occur in all other Boloceroididae. The capsular content consists of a typical shaft but the thread is short, very thin, and difficult to see. When the nematocyst is observed discharged, there is usually no thread at the end of the shaft. However, careful examination of the interior of the capsule reveals the thread to be adhering to the blind end of the capsule. After watching many of these nematocysts discharge it became quite evident that the thread sticks fast to the capsule wall. Before discharge of the capsular content the thread has a characteristic loop, and as the expulsion of the shaft begins the loop can be seen to draw taut. As evagination progresses the thread always (?) breaks from the shaft and the thread springs back just as it was before discharge. At present it is unexplainable why the thread is attached to the capsule of this type of nematocyst. The fact that the thread remaining in the capsule after discharge is the same length as before discharge is not necessarily inconsistent with the folded nature of the shaft described under general considerations of the cnidae. The thread of this particular type of microbasic *p* breaks at the folded end of the shaft (the notch) rather than the tip, probably due to constriction at this point, and the part within the shaft apparently is pinched so that in most cases it is not evaginated on discharge. The thread is so fine it cannot be readily discerned within the lumen of the shaft but on occasion part is evaginated with the shaft.

Microbasic *p*'s were also observed in several instances to have threads so nonrefractive as to be easily overlooked with ordinary illumination (Fig. 6, *f*). Threads of this type have considerable caliber (up to ¼ that of the shaft) but have walls so thin as to be transparent. The most common reason the threads are overlooked in those nematocysts that have been called amastigophores is that they are sometimes very short (Fig. 1, *e* and Fig. 6,

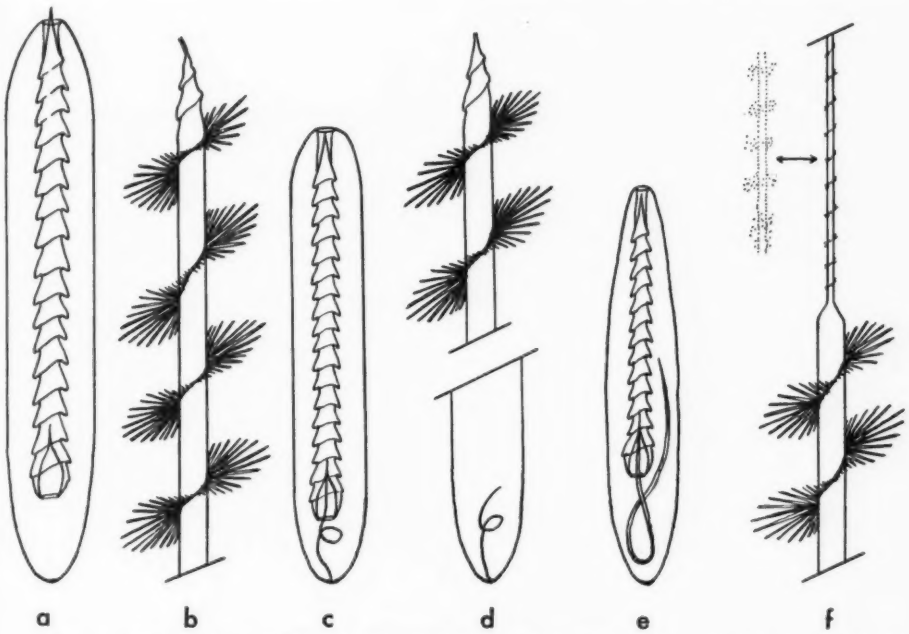

FIG. 6. Microbasic *p*-mastigophores, formerly called microbasic amastigophores. (*a,b*) *Actinothöe;* (*c*) *Bunodeopsis;* (*e,f*) *Macranthea;* (*d*) thread stuck to end of empty capsule and evaginated shaft without thread from same nematocyst, *Bunodeopsis.*

a,b). There must be some agreement as to the length of tube that constitutes a thread. If nematocysts with shafts tipped with a very short thread are to be considered distinctly different from those with long threads, then the former could conceivably be called amastigophores. However, this would be an arbitrary decision, there being neither a clear-cut morphological nor distributional distinction. There are certain genera, particularly in the Acontiaria, that characteristically possess microbasic *p*'s with vestigial threads in addition to those with distinct threads. But because these nematocysts with a short thread intergrade with the typical microbasic *p*'s and have a random distribution in the Anthozoa there is little to be gained by placing them in a separate category. It is therefore proposed to eliminate the category, microbasic amastigophore, and regard the nematocysts so designated as microbasic *p*-mastigophores.

The capsules of the microbasic *p*'s are almost always pyriform to elliptical in shape and their diameters are usually two or more times those of basitrichs or microbasic *b*'s of comparable length. The capsules vary greatly in size, some being less than 5μ, others exceeding 100μ.

Microbasic *p*-mastigophores occur most abundantly in the filaments, acontia, and actinopharynx but certain species lack them in one or more of these organs. Some species also possess them in the tentacles and column but there they are never as numerous as in the entodermal organs. The distribution of the microbasic *p*'s within the Anthozoa is rather uniform except for the orders Octocorallia and Ptychodactiaria where they are absent.

Microbasic q-*mastigophores* (*New Category*)

Iwanzoff (1896) was apparently the first to describe and figure the dart-like structure associated with the capsular content of certain mastigophores. He attributes the darts found in conjunction with these nematocysts from *Aiptasia diaphana* to the fusion of some of the armature shed from the nematocysts' tubes. Weill (1934) also is convinced that the dart represents part of the deciduous armature from the shaft which has become agglutinated. His Figures 122–125, p. 144, show several aspects of the dart from *Actinoloba* (= *Metridium*) *dianthus*. Two of the three darts shown in his Figure 123 are probably from two adjacent nematocysts and do not represent a case of several darts coming from a single capsule or a single dart becoming disassociated as he proposes. Iwanzoff and Weill consider the darts to be somewhat of an anomaly among nematocysts. The interpretations of both men are rather illogical, for it is difficult to conceive how the sloughed armature from the shafts of the nematocysts could become reorganized on every occasion to form the precise structure of the dart. It seems more reasonable to consider the dart an unattached, discrete structure consistently a part of the capsular content of certain kinds of nematocysts. Figure 7, *a–d* represents diverse aspects of the darts from the acontia of *Aiptasia pulchella*. The dart (Fig. 7, *a*) is discernible within the lumen of the undischarged shaft where it neatly fits over the end of the folded part of the shaft. On discharge of the nematocyst the dart is ejected and pushed aside by the evaginating tube. Once free of the capsule the fine, transverse striations (probably armature) are visible on the dart (Fig. 7, *d*). In addition to the observations on the dart, the fact that the tubes of the discharged nematocysts retain their armature rather conclusively discounts the theory of the dart's being formed from sloughed armature. Further,

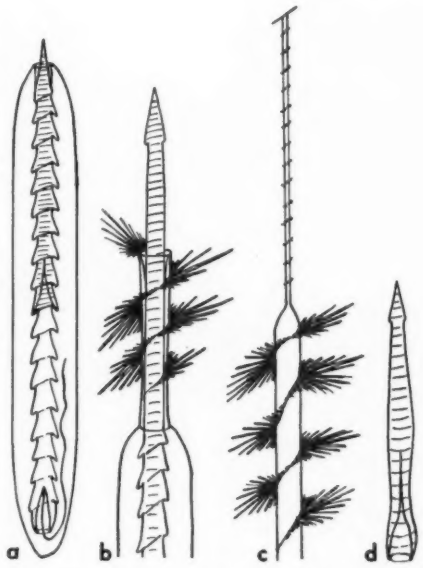

FIG. 7. Microbasic *q*-mastigophores from *Aiptasia*. (*a*) undischarged nematocyst; (*b*) beginning of evagination; (*c*) shaft of same nematocyst with thread; (*d*) dart from same nematocyst.

the presence of the thread on the discharged shaft rules out an alternative hypothesis that the dart is a portion of the shaft. Although the derivation of the dart is unknown at present, there can be little doubt the dart is a real and innate structure peculiar to certain microbasic mastigophores. Therefore, it is proposed to call those nematocysts with a shaft less than three times the length of the capsule and abruptly reducing to a thread, and with a detachable dart on the end of the invaginated shaft, microbasic *q*-mastigophores.

The survey of microbasic *q*-mastigophores is extremely incomplete. In the few species of actinians found to possess microbasic *q*'s, the nematocysts seem to be restricted to the acontia. At the present time microbasic *q*'s are known to occur in only four species of *Aiptasia* and one species of *Metridium*, but now that these nematocysts have been redescribed in a

new light many species of actinians, particularly Acontiaria, are likely to be found to have them.

Macrobasic p-*mastigophores* (*New Category*)

In the category, macrobasic *p*-mastigophores, it is proposed to include those nematocysts with a shaft which is more than three times the length of the capsule and which is abruptly reduced to a thread. The shaft in the undischarged condition is invaginated and folded back within itself. The armature of the shaft is distinctly longer than that of the thread. The shaft may have a diameter only slightly greater than the thread, causing the juncture of the shaft and thread to be obscure. This definition includes the macrobasic amastigophores (Fig. 8, *a,b*) and some holotrichs (Fig. 8, *c–g*) of Weill and Carlgren.

Macrobasic amastigophores were examined from all actiniarian families reported to possess them and were found to have threads. Although the threads are very short (e.g., Fig. 1, *e*), their presence distinguishes these nematocysts as *p*-mastigophores, and because the shafts are more than three times the length of the capsule, a new category, macrobasic *p*-mastigophores, is erected for them. The shafts of these nematocysts are of variable length and within the capsule may correspondingly form one to several longitudinal coils. The nematocysts are refractory to stain and the tube evaginates reluctantly. Carlgren (1940 and 1949) attributes macrobasic amastigophores to only the actiniarian families Aliciidae and Diadumenidae. However, I have found this type of nematocyst (now referred to as macrobasic *p*'s) in the Boloceroididae (Fig. 8, *a*) and rarely in the Aiptasiidae. Upon closer inspection they will likely be found in other families of Actiniaria. The macrobasic *p*'s occur in the ectoderm of the column, where they usually are restricted to the vesicles, but in the Diadu-

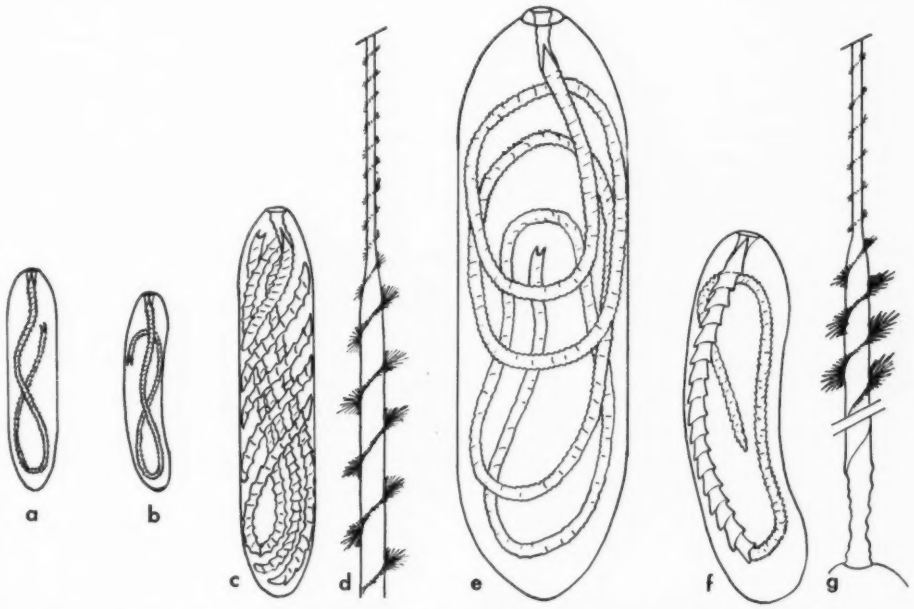

FIG. 8. Macrobasic *p*-mastigophores. (*a*) *Bunodeopsis;* (*b*) *Alicia;* (*c,d*) *Corynactis;* (*e*) *Rhodactis;* (*f,g*) *Cerianthus.*

menidae they are found in the ectoderm of the tentacles (catch tentacles excepted). The rarity of this type of nematocyst, its spotty distribution in the Anthozoa, its short thread, and its reluctance to evaginate suggest it may be a relic in the Actiniaria.

In addition to the macrobasic *p*-mastigophores just described, there are certain large nematocysts (Fig. 8, *c–g*) found in the Corallimorpharia and Ceriantharia which have heretofore been called holotrichs but, unlike holotrichs, have a tube that is divisible into a shaft and thread. The reason they have been considered holotrichs may be that the tube is usually very long and the slight demarcation between shaft and thread is overlooked. The shaft may be 4 to 30 times the length of the capsule and be reduced to a thread which is sometimes more than two-thirds the diameter of the shaft. Similar nematocysts with a shaft 4 to 6 times the length of the capsule (Fig. 8, *f,g*) have been consistently called haplotelic microbasic *b*-mastigophores by Weill and Carlgren. Unlike microbasic *b*'s which sometimes have a distinctly differentiated shaft (Fig. 4, *k,l*) but which are simply invaginated within the capsule, these nematocysts (Fig. 8, *f,g*) have a shaft that is invaginated and folded within itself. They therefore resemble *p*-mastigophores and not *b*-mastigophores. There is frequently present a rather long tube (the proximal portion of the shaft) (Fig. 8, *e*) between the capsule aperture and the point of the shaft. This arrangement of the capsular content and the V-shaped notch at the folded end of the tube is identical to the configuration of the undischarged contents of *p*-mastigophores. Because this nematocyst has a shaft more than three times the length of the capsule and folded within itself, it is referred to the category, macrobasic *p*-mastigophores.

The armature of the shaft of large macrobasic *p*'s is never as long and coarse as that on the shafts of other *p*-mastigophores but it is usually about twice as long as the armature on the thread. The tube of these large macrobasic *p*'s is apparently thin-walled, for when it evaginates it becomes considerably inflated, causing it to lengthen and sometimes attain a diameter of 15μ or more near the base. Such distension causes the bands of armature to become separated and the tube to appear rather bare. Frequently the shaft is unarmoured proximally for as much as two-thirds of its length. In addition, the armature seems to be deciduous and when it is lost the tube appears like that of an atrich. It is possible some of the very large atrichs described from cerianthids and corallimorpharians are macrobasic *p*'s which have lost their armature. The thread of the large macrobasic *p*'s is usually approximately the length of the shaft. Being thin-walled it is inflated when evaginated and in spite of its considerable diameter is difficult to discern.

The large macrobasic *p*-mastigophores are a major element of the cnidoms of Ceriantharia and Corallimorpharia. They occur in all nematocyst-bearing organs and in either the ectoderm or entoderm.

The group of nematocysts comprising the category, macrobasic *p*-mastigophores, may seem heterogeneous because the nematocysts vary in size and have different distributions. However, the nematocysts of the group are very similar structurally. The large nematocysts of the category form an element of the anthozoan cnidom which is well represented in the seemingly more ancient Ceriantharia and Corallimorpharia. Their smaller counterpart, on the other hand, may represent a rare relic in the apparently more recent order Actiniaria.

Holotrichs, Weill 1930

The holotrichs are those nematocysts with a tube of uniform diameter which is uniformly armoured throughout its length. They are typically long, thin capsules with a neat and completely coiled content (Fig. 9, *a–d*). They sometimes have very fine armature on the tube

which, if overlooked, results in confusion of these nematocysts with atrichs. Usually the long, thin nematocysts of the marginal spherules (acrorhagia) are described as atrichs. All marginal spherules I have examined contained holotrichs but no atrichs. Likewise, the nematocysts in the tentacles of the *Sagartiomorphe* (Fig. 9, *d*), which Carlgren (1949) mistakenly calls atrichs, are holotrichs. The long, thin holotrichs seem to be a product of the ectoderm. They occur chiefly in the marginal spherules and tentacles and rarely in the column of actiniarians. It is doubtful if they occur in other orders of Anthozoa.

The assemblage of nematocysts called holotrichs is heterogeneous, the category probably being a catch-all for several types which we are at present unable to separate satisfactorily. In the discussion of the preceding category I have shown that some are macrobasic *p*-mastigophores. However, there remains at least one type to be considered. These nematocysts (Fig. 9, *e–i*) are the very large, broad ones found in the Ceriantharia, Corallimorpharia, Zoantharia and young forms of certain Actiniaria. Although this type of nematocyst has a tube like that of a holotrich, it is different in other respects. This nematocyst has a different distribution, it is broader and larger, the coiling of the tube is loose and irregular, it is refractory to stains, and evaginates differently. A clue to the identity of this nematocyst may be gained from an investigation of cnidogenesis in the Anthozoa. Although the data on cnidogenesis are very incomplete, large nematocysts resembling Figure 9, *f* have been found in the larvae and young of several species of Actiniaria. These nematocysts are always a very short-termed element of the species' cnidoms and have never been found in the adults. These observations suggest that the large holotrichs (?) may be a generalized prototype of all other nematocysts. However, the evidence seems insufficient to warrant the erection of a new category for them; thus (with reservations) I prefer to retain them in the holotrich category.

The large holotrichs (Fig. 9, *e–i*) are found in both the ectoderm and entoderm of Ceriantharia, Corallimorpharia, Zoantharia, and Scleractinia and are present in almost all the nematocyst-bearing organs.

Atrichs, Weill 1930

The atrichs are defined as nematocysts with an unarmoured tube of uniform di-

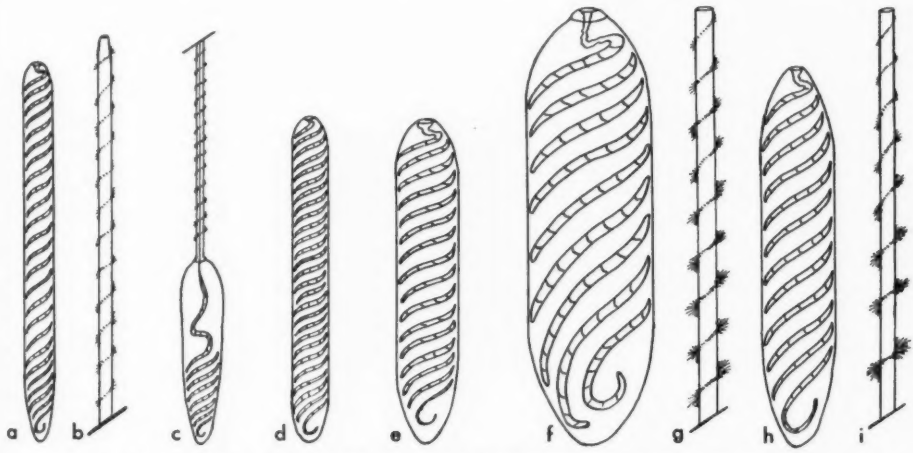

FIG. 9. Holotrichs. (*a,b*) *Anthopleura;* (*c*) *Diadumene;* (*d*) *Sagartiomorphe;* (*e*) *Cerianthus;* (*f,g*) *Zoanthus;* (*h,i*) *Fungia;* (*b,g,i*) tips of evaginated tubes.

ameter. The atrich category, like that of the holotrichs, seems to be comprised of two types, a small variety found only in the Actiniaria and a larger variety found in the Ceriantharia, Corallimorpharia, and Zoantharia.

The small atrichs (Fig. 10, *a,b*) are broad nematocysts with a very long tube which is coiled somewhat elongately in the capsule. They take up methylene blue, and the tube evaginates readily. The small atrichs are known only from the ectoderm of catch-tentacles of species of the family Diadumenidae. Atrichs described for other Actiniaria have proved to be either basitrichs or holotrichs and are discussed under these categories.

The large atrichs (Fig. 10, *c,d*)differ from the small ones in the following respects. They are frequently more than twice the length of the small ones but in proportion are not so broad. The tube is more transversely coiled in the capsule and evaginates with reluctance. The nematocysts are refractory to methylene blue and acid fuchsin. They occur in the ectoderm and entoderm of most nematocyst-bearing organs of Ceriantharia, Corallimorpharia, and Zoantharia.

The tubes of the large atrichs evaginate so rarely that few details of the tube are known. On several occasions what appeared to be fine, sloughed armature was found in conjunction with crushed nematocysts resembling large atrichs. An investigation of the development of these nematocysts might indicate possible relationships with other types. However, until we have more data on these nematocysts it seems best to consider them atrichs.

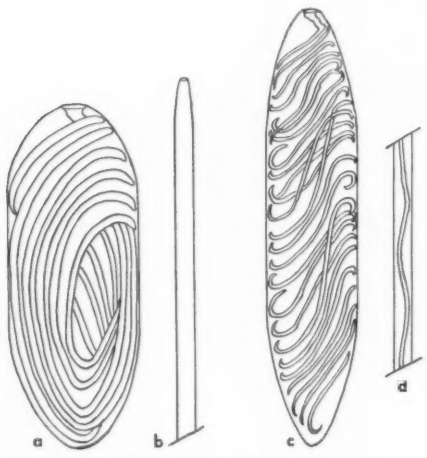

FIG. 10. Atrichs. (*a*) *Diadumene;* (*b*) tip of evaginated tube, *Diadumene;* (*c*) *Cerianthus;* (*d*) portion of invaginated tube in lumen of evaginated tube, *Cerianthus.*

Summary and Conclusions

The enduring and varied features of nematocysts make them an excellent potential index to the phylogeny of the Coelenterata. Through the efforts of Robert Weill and Oskar Carlgren the nematocysts of the Coelenterata have been classified and demonstrated to be of systematic value. However, when species for which one or the other of these men had determined cnidoms were examined, the nematocysts were frequently found to be different than reported. The incongruity of my observations with theirs led to the belief that some types of nematocysts had been misinterpreted for one or more reasons. The principal difference of interpretation proved to be of the finer structures of the nematocysts, e.g., the armature on the thread, or the configuration of the contents of the capsules. The discernment of such features is frequently contingent on the quality of the microscope, the magnification, and the investigator's visual acuity. A survey was made of representatives of all but one order (Ptychodactiaria) of Anthozoa to establish criteria for the recognition of nematocysts of the class which would be less dependent on these variables.

On the basis of the survey two new categories (microbasic *q*-mastigophores and macrobasic *p*-mastigophores) are proposed. Two categories (micro- and macrobasic amastigophores) are eliminated. The reappraised and new categories are:

1. Spirocysts. Acidophilic nematocysts with a tube of uniform diameter which bears armature of uniform length throughout.

2. Basitrichs. Nematocysts with a tube of uniform diameter which bears coarse armature proximally for a distance less than three times the capsule length.

3. Microbasic *b*-mastigophores. Nematocysts with a proximal shaft which is less than three times the capsule length and which is indistinctly reduced to a distal thread. There is armature on the shaft which is distinctly longer than that on the thread.

4. Microbasic *p*-mastigophores. Nematocysts with a proximal shaft less than three times the capsule length and abruptly reduced to a distal thread. The armature of the shaft is distinctly longer than that of the thread. The undischarged shaft is invaginated and folded back within itself.

5. Microbasic *q*-mastigophores. Nematocysts with a proximal shaft which is less than three times the capsule length, which is abruptly reduced to a distal thread, and which bears armature distinctly longer than that of the thread. The shaft is doubly invaginated within the capsule and has an unattached dart over its tip.

6. Macrobasic *p*-mastigophores. Nematocysts with a proximal shaft which is more than three times the capsule length, which is abruptly reduced to a thread, and which has armature distinctly longer than that of the thread. The shaft within the capsule is doubly invaginated.

7. Holotrichs. Basophilic nematocysts with a tube of uniform diameter bearing armature of uniform length throughout.

8. Atrichs. Nematocysts with a smooth tube of uniform diameter.

The macrobasic *p*-mastigophores and holotrichs each seem to be heterogeneous assemblages of nematocysts, but there is insufficient evidence to segregate them into more homogeneous categories.

The effect of alterations in the categories of cnidae on anthozoan systematics must be further evaluated. It is unlikely that radical changes in the phylogenetic arrangement of the members of the class would be necessary, for nematocysts are far from being the only criterion upon which anthozoan systematics is based. It is hoped that a more immediate consequence of the re-interpretation of the cnidae will be a simplified and more consistent identification of types of nematocysts.

LITERATURE CITED

BEDOT, M. 1890. Observations sur les nématocystes. *Arch. Sc. phys. nat. Genève, 22*:606–608.

——— 1896. Note sur les cellules urticantes. *Rev. Suisse de Zool., 3*(4):533–539.

CARLGREN, O. 1900. Ostafrikanische Actinien. *Jahrb. Hamburg wiss. Anstalt, 17*(2).

——— 1924. On *Boloceroides, Bunodeopsis* and their supposed allied genera. *Arkiv f. Zoologi, 17a*(1):1–20.

——— 1940. A contribution to the knowledge of the structure and distribution of the cnidae in the Anthozoa. *Lunds Univ. Årsskrift N.F. (2), 36*(3):1–62.

——— 1945. Further contributions to the knowledge of the cnidom in the Anthozoa especially in the Actiniaria. *Lunds Univ. Årsskrift N.F. (2):41*(9):1–24.

——— 1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. *K. Svenska Vet. Akad. Handl., 1*(1):1–121.

GOSSE, P. H. 1860. British sea-anemones and corals (Actinologia Britannica). Van Voorst, London. 362 pp.

IWANZOFF, M. 1896. Über den Bau, die Wirkungsweise und die Entwicklung der Nesselkapseln der Coelenteraten. *Bull. Soc. Nat. Moscou, N.S., 10*:95–161 and 323–355.

MOEBIUS, K. 1866. Über den Bau, den Mechanismus und die Entwicklung der Nesselkapseln einiger Polypen und Quallen. *Abhdln. naturw. Ver. Hamburg, 5*(1):1–22.

WEILL, R. 1930. Essai d'une classification des nématocystes, des Cnidaires. *Bull. Biol. Fr.-Belg., 64*:141–153.

——— 1934. Contribution à l'étude des Cnidaires et de leurs nématocystes. *Trav. Stat. Zool. d. Wimereux*, 10, 11. 701 pp.

WILL, L. 1909. Die Klebkapseln der Aktinien und der Mechanismus ihrer Entladung. *Sitzb. Abhdln. naturf. Ges. Rostock, N.F.* 1. 39 pp.

CHARLES E. CUTRESS is a doctoral candidate, Department of Zoology and Entomology, University of Hawaii, Honolulu. An abbreviated account of this work was presented at the Society of Systematic Zoology section of the December 1954 meeting of the American Association for the Advancement of Science in Berkeley, Calif. Contribution No. 74 from the Hawaii Marine Laboratory, in cooperation with the Department of Zoology and Entomology, University of Hawaii.

On Scientific Terminology

OTTO HAAS

COMPOSITION OF SCIENTIFIC WORDS. By Roland Wilbur Brown. Published and distributed by the author at U.S. National Museum, Washington 25, D. C., 1954. 882 pp. $8.00.

THE LANGUAGE OF SCIENCE. ITS GROWTH, CHARACTER AND USAGE. By Theodore H. Savory. (In: *The Language Library, ed. by Eric Partridge.) London, Andre Deutsch, 1953. 184 pp. 10s 6d.*

THE purpose and usefulness of the first of these two books, whose author is a Geologist of the U.S. Geological Survey and Paleobotanist at the U.S. National Museum, are best indicated by its subtitle: "A manual of methods and a lexicon of materials for the practice of logotechnics."

The main part, a "Cross-Reference Lexicon" of 814 pages, is preceded by an Introduction of 55 pages which, after a lucid exposition of the evolution and the peculiarities of the English language, attempts, under the heading "Nature of Greek and Latin," to familiarize the reader without proper classical training with the essentials of transliteration from, and the grammar of, those languages. The following section, entitled "Formation of Scientific Terms," contains instructions in logotechnics (or word coining) proper and thus constitutes the core of the book. The author's general postulate that scientific words "should be simple, euphonious, pure and mnemonically attractive, to say nothing of being descriptively appropriate," well deserves to be quoted in full, as does his appeal to biologists in particular that "if a plant or animal is worth describing it surely merits an appropriate, uncriticizable name, and the sacrifice of a little time and energy by the creator in devising such a name. He should find this not only a challenge to his ingenuity, but, in subsequent years, a recurrent pleasure like that brought by all significant, creative work."

Dr. Brown distinguishes three modes of creation of scientific terms: adoption, composition, and arbitrary creation of words. His most explicit instructions deal with the composition of words.

As to Latinization, Dr. Brown seems inclined to allow more liberty to authors than this reviewer would. Concerning the formation of genitives indicating commemoration or dedication he sticks to the letter of Art. 14, paragraph 3, of the Rules of Zoological Nomenclature even where such strict adherence leads to forms like *"clusiusi"* instead of *"clusii."* Of these two, the latter sounds much more euphonious to the reviewer. Nobody familiar with biological nomenclature will be surprised to find that the author deemed the problems of gender, especially the requirement of adjustment of the two terms of a binomial to one another, important enough to devote a separate section to them (pp. 50–54).

The Cross-Reference Lexicon aligns not only Greek and Latin synonyms but also those in other languages, both living and dead, with the English key words; thus, it accumulates an immense wealth of information on the meaning and etymology of several thousand terms. It furnishes the material to which to apply the directions so well expressed in the Introduction. A bibliography of nearly 130 titles provides a welcome guide to supplementary reading, and a concise index facilitates the use of the book.

All biologists should assign Brown's volume a place of preference on their shelf of reference books. The few who do not actually need it will all the same thoroughly enjoy browsing through it.

The many who do need it should carefully consult it every time before proposing a new name.

The second book, much thinner than the first, is not intended, as is Dr. Brown's work, to give immediate practical help to taxonomists in search of suitable names, but is essentially historical and semasiological in character.

The introductory chapters deal with the origin of scientific terms, emphasizing the high percentage of those derived from Latin and Greek roots and differentiating between borrowed, imported, and invented words. The book then discusses the growth and the character of the language of science, justly pointing out that in scientific usage "the meaning is the only matter of importance" and that, thus, "the scientist is debarred . . . from using any devices that lead to graciousness in writing" and "must from the outset abandon all thoughts or hopes of achieving eloquence." So conceived, scientific prose should be clear, intelligible, if allowance is made for inevitable specialization, and cold. Of the three concluding chapters, the first deals with the vocabularies of the sciences, tracing many scientific terms back to their first uses; the second, with the scientists and their languages, comparing the percentages of the most important languages in scientific literature; and the last, with the literature of science, listing some scientific works considered particularly important.

Although this book by a prominent British arachnologist is focused on England, as would be expected, American readers will be pleased with the author's benevolent attitude toward "Americanisms" (pp. 27–28). Beyond that, *The Language of Science* should make fascinating reading for anybody interested in linguistics or science and, especially so, for those interested in both fields.

OTTO HAAS is Associate Curator Emeritus of Fossil Invertebrates at the American Museum of Natural History, New York City.

Not the Superspecies

(Concluded from p. 144)

specific distinctions probable, will be a (Mayrian) superspecies.

In fact, the two concepts of the geographical and chronological superspecies, according to their definitions, have in common only that (like most genera, families, etc.,) they are monophyletic groups containing more than one species. But one is the result of a diverging group of allopatric lineages, the other is a part of a single lineage. It is perfectly true that, as Sylvester-Bradley states, the neontologist and the palaeontologist separately see only part of the picture; but that picture is not of a single superspecies in space and time, but of evolution proceeding within a single natural group undergoing cladogenesis. Certainly both the chronological and the geographical superspecies are aspects of that—no one has denied it.

CAIN, A. J. 1953. Geography, ecology and coexistence in relation to the biological definition of the species. *Evolution, 7*:76–83.

——— 1954*a*. Animal species and their evolution. Hutchinson's University Library, London.

——— 1954*b*. Subdivisions of the genus *Ptilinopus* (Aves, Columbae). *Bull. Brit. Mus. (Nat. Hist.), 2*:265–284.

MAYR, E. 1931. Notes on *Halcyon chloris* and some of its subspecies. *Am. Mus. Novit.*, No. 469.

——— 1942. Systematics and the origin of species. Columbia Univ. Press, New York.

SYLVESTER-BRADLEY, P. C. 1951. The subspecies in palaeontology. *Geol. Mag., 88*:88–102.

——— 1954. The superspecies. *Syst. Zool., 3*: 145–146, 173.

A. J. CAIN
Dept. Zoology and Comp. Anatomy
Oxford University
Oxford, England

Points of View

Subspecific Nomenclature: The Proposed Method of Wilson and Brown

While Wilson and Brown usefully comment on the inconclusiveness of character-analysis in the study of animal populations below species level, little of what they write bears on the strict issue of whether a Latin trinomen is "inefficient and superfluous for reference purposes" when compared with their alternative suggestion of a Latin binomen plus "the simple vernacular locality citation or a brief statement of the range involved."

Those of us who are willing to accept *"R. pipiens,* southeastern corner of J. B. Smith farm, 5 miles west of Montauk Pt. in cattail swamp" as the "kind of reference shorthand we shall need" to apply the system of Wilson and Brown, must concede that *"R. pipiens* Montauk A" sounds a little more terse and efficient. But it does not indicate what is the reference shorthand to use at the extreme limit of the Montauk A range on set 1 characters, set 2 characters, and set 3 characters, supposing set 1 fade out five miles west of Montauk Pt. and 35 to the east, set 2 persist for 50 miles west and at least 35 to the east, and set 3 for 100 miles on either side. If author A, working with all three sets, defines 5 miles west of Montauk Pt. and 35 miles east as the limit of Montauk A, what should he call the population six miles west? Is it termed "intergrade Montauk A-Long Id. D" or given a noncommittal new vernacular locality name?

Use of *vernacular* names either does or does not presuppose transliteration. If in this case it does not, are we asked to believe that a locality cited, say, in Tibetan characters is more convenient to most of us than a Latin name? If transliteration is mandatory, is "Mt. Pairot," for example, interchangeable with "Mt. Beirut," or "Mt. Tolenkiup" with "Mt. Dolennankap"? The difficulty can, of course, be sidestepped. Thanks to one of the "appealing characteristics" of an "informal and flexible vernacular system," we have only to trace the population bearing the awkward name over into an adjoining area and we are compelled to change the name—(e.g. "Lhasa" to "Tibetan Plateau"). In considering the example given by Wilson and Brown, one is compelled to wonder just how many name-changes would be involved in the transition from the locality "Lhasa" to that of "Tibetan Plateau" as the third name indicating a population of mice with a black cheek-stripe.

To the writer, a Latin name (such as *lhasensis*), once given, would always mean the monophyletic black-cheek-striped mice of Central Asia, even if one of them turned up in a collection from Burma, so long as it agreed with the characters cited. A single Tibetan vernacular name *could* mean just as much—no more. But even *stable* vernacular names in a multiplicity of languages are not more efficient than a stable name in one familiar language such as Latin. (One can at least detect misprints in Latin!) But faced with the thought of grappling with a *series* of ephemeral Tibetan vernaculars written by Tibetan or Chinese taxonomists, all, at various times, indicating the same population (if we assume no doubtful synonymy or misidentified races), non-systematic zoologists may be tempted to summarize their views about the proposed method of Wilson and Brown in "frankly expressive" informal and flexible vernacular.

Wilson, E. O., and Brown, W. L. 1953. The subspecies concept and its taxonomic implication. *Syst. Zool.*, *2*:97–111.

——— 1954. The case against the trinomen. *Syst. Zool.*, *3*:174–176.

R. G. Fennah
Imperial College of Tropical Agriculture
St. Augustine, Trinidad, B. W. I.

Postscript to a Survey of Infraspecific Categories

In 1940, in connection with discussions of categories lower than species, the writer published the results of a survey of proposals of new infraspecific names by North American entomologists for the preceding 50 years (1890–1939) ("Entomological usage of subspecific names," *Ent. News*, Vol. 51, pp. 159–164). The survey covered approximately 750 volumes of 21 standard American serials devoted entirely or in considerable part to taxonomic entomology. One small phase of the survey was not published, and is now recorded for whatever interest it may have. Comparable data for the years 1940–49 have recently been compiled in order to carry the information through the last complete decade.

Table I summarizes by decades the proposals of new infraspecific names. Races have been included in the subspecies column, because an interpretation of infraspecific categories in terms of populations would unquestionably accept race as a subspecific population unit. The number so proposed is only a minor factor, there being 7, 2, 8, 54, 19, and 45 in the six decades covered by the table.

It is noteworthy that since 1910 there has been little difference per decade in the total numbers of names proposed as variety and as subspecies, but a steady change in the relative proportions. One can only speculate whether this is due to changes in underlying principles or to an increasing awareness of the possibility of strict interpretation of the term "subspecies" in the International Rules of Zoological Nomenclature, or to some combination of the two. The figures for the last decade could scarcely have been affected by the plan for infraspecific categories adopted at the Paris Congress in August 1948, but they might well have been influenced by the lively discussion of the subject from about 1936 to 1940 by Riley, Hovanitz, Sabrosky, and others.

Of the 1538 new varieties and 1210 new subspecies having locality data sufficiently definite to permit tabulation, 64.6 percent of the varieties (993) and 57.2 percent of the subspecies (693) were based on material from single localities. Furthermore, of those whose definite specimen data permitted tabulation, it was found that 26.4 percent of the new varieties (274 out of 1038) and 18.7 percent of the new subspecies (184 out of 984) were founded on single specimens. The record for subspecies does not harmonize well with definitions involving such features as "adjoining range" and "zone of intergradation."

As shown in Table II, the percentage of names based on a single locality has dropped rather steadily, the few deviations from a downward trend being slight and probably of little consequence. For both variety and subspecies the trend and

TABLE I —NEW INFRASPECIFIC NAMES, 1890–1949

DECADE	VARIETY	SUBSPECIES	TOTAL, VARIETY + SUBSPECIES	ALL OTHERS
1890–99	104	13	117	11
1900–09	266	71	337	4
1910–19	443	218	661	27
1920–29	428	247	675	257
1930–39	281	287	568	94
1940–49	136	519	655	52
Totals	1658	1355	3013	445

TABLE II—PERCENT OF NEW INFRASPECIFIC NAMES BASED ON A SINGLE LOCALITY

	VARIETY		SUBSPECIES	
DECADE	TOTAL	PERCENT ON ONE LOCALITY	TOTAL	PERCENT ON ONE LOCALITY
1890–99	95	89.4	6	83.3
1900–09	255	70.6	61	86.8
1910–19	416	71.1	206	71.3
1920–29	379	55.6	177	59.3
1930–39	258	55.8	244	55.3
1940–49	135	57.0	516	48.1
Total	1538	64.6	1210	57.2

the proportion have been approximately parallel. But even after the steady decrease, approximately half the names proposed in the last decade were based on single localities.

Whether taxonomists decide to call infraspecific populations by formal Latin trinomials, symbols, or vernacular designations, they should offer better justification than the meager evidence of a single specimen or a single locality when proposing to recognize such a population unit as a subspecies. Surely taxonomists in general cannot agree with the statement of one famous entomologist, in naming a new subspecies no longer ago than 1933: "I treat this as a subspecies, having only one specimen"!

CURTIS W. SABROSKY
Entomology Research Branch
Agricultural Research Service
U.S. Dept. of Agriculture

How Many Species?

Obtaining accurate figures of the number of described species of invertebrate groups appears to be a matter of great, almost insuperable, difficulty. Many of the published figures, especially those appearing in college textbooks of zoology, are of little value, as they are simply copied from each other. The tabulation of Muller and Campbell in the December 1954 issue of SYSTEMATIC ZOOLOGY falls wide of the mark in several instances. A figure of 6000 for the Platyhelminthes is far too low. As a specialist on the Turbellaria I keep a card catalogue that at least attempts to list all described species. A count in this catalogue reveals over 3000 described species of Turbellaria. From the data in Wardle and McLeod's *The Zoology of Tapeworms* (1951) one may estimate at least 2000 described species of tapeworms. A figure for trematodes was obtained as follows. Braun in his account of trematodes in Bronn's *Klassen und Ordnungen des Tierreichs* gave figures of 117 Monogenea and 570 Digenea as of about 1890. Counts in the *Zoological Record* for the years 1891 to 1951, inclusive, yielded a total of 4460 new species of trematodes described in sixty years, and adding Braun's figure of 687, one arrives at a total of over 5100 described species of trematodes as of 1951. Therefore it is clear that there are at least 10,000 described species of existing Platyhelminthes rather than the 5000 to 7000 usually given.

Muller and Campbell's figure of 6000 for the Nematoda is also seriously underestimated. In my book, *The Invertebrates*, Vol. III, p. 57, I gave grounds for an estimate of 9000 described species of existing nematodes as of 1950. The figure may be supposed to have risen to 10,000 at the present time, and even this figure is probably a little low.

Muller and Campbell's figure of 950 for the existing echinoderms is simply fantastic. Dr. Elisabeth Deichmann, world specialist on holothurians, has informed me that there are 500 species of sea cucumbers "if one is a lumper" and 700 "if one is a splitter." A count in Mortensen's *Monograph of the Echonoidea* yielded 750 described species of sea urchins. H. L. Clark's book *The Echinoderm Fauna of Australia* gives figures of 1700 for the species of ophiuroids and 1200 for the species of asteroids, as of 1946. However, Dr. Ailsa Clark, a specialist on asteroids, has told me she thinks 2000 a more nearly correct figure for asteroids at present, and no doubt 1700 is rather low for ophiuroids as they are the most numerous of all groups of echinoderms. In his *Monograph of the Existing Crinoids* A. H. Clark gave the number of present crinoids as 660. We therefore arrive at a figure of around 5000 as the minimum number of described species of existing echinoderms. Muller and Campbell's figure of 4050 for extinct echino-

derms is also very poor. Durham (*Bull. Mus. Comp. Zool. Harvard, 112,* 1954) lists 7800 extinct Eleutherozoa; Moore, Lalicker, and Fischer in *Invertebrate Fossils* (1952) list about 5000 extinct crinoids (p. 635); and from Bassler and Moody's *Bibliographic and Faunal Index of Palaeozoic Pelmatozoan Echinoderms* (1943), one may estimate nearly 900 extinct non-crinoid Pelmatozoa. This makes a total of 13,700 extinct species of echinoderms. A figure of 40,000 to 50,000 is probably nearer the truth for the existing species of chordates than the 33,640 estimate of Muller and Campbell. All of the foregoing figures omit varieties, subspecies, and larval forms.

However, even the most accurate figures obtained by painstaking counts in original sources are illusory. In the first place, such counts are merely a list of names; it is impossible to know how many of these names are valid. In the second place, the invertebrate fauna of the world, with the exception of arthropods, is so poorly known that such figures give a wrong picture of the actual number of animal species. For instance, the figure of 10,000 nematodes is probably not even 10 percent of the existing species of nematodes. Similarly it is probable that not even 25 percent of the existing Platyhelminthes have been described; as presumably every vertebrate is afflicted with at least one species of trematode, it seems probable that there are, anyway, 40,000 existing species of trematodes. As a specialist on the Turbellaria I may say that no end is in sight of the number of free-living flatworms. Every collection that is received for identification consists largely of new species. One may suppose that new species of invertebrate fossils are constantly unearthed. At present a comparison of the number of extinct and living species of animals seems rather useless.

Nevertheless, good data are always welcome. Specialists should come forward with counts of the number of species in their groups. An invitation to this effect was already extended by Sabrosky in the September 1953 issue of SYSTEMATIC ZOOLOGY and I can only heartily second the motion.

LIBBIE H. HYMAN
American Museum of Natural History
New York 24, N. Y.

Not the Superspecies

I have criticised Sylvester-Bradley's proposal (1951) that a single palaeontological lineage composed of a succession of full species should be called a superspecies because to do so "obscures two totally different concepts under the same name" (Cain, 1953). Sylvester-Bradley disagrees (1954) and brings forward some interesting arguments to show that the two concepts (his, and the *Artenkreis* for which the term superspecies was introduced by Mayr) are essentially the same. However, Sylvester-Bradley's contentions are based in part on errors of statement. It is not true that Mayr has defined the *geographical superspecies* nor that Sylvester-Bradley has defined the *chronological superspecies,* as he claims. Both authors (Mayr, 1931, p. 2; 1942, p. 169; and Sylvester-Bradley, 1951, p. 98) have defined the *superspecies,* with no qualifying adjectives whatever. This is what any serious worker must consider objectionable—the use of exactly the same word, with no qualifications, for on the one hand an array of monophyletic, geographically representative species existing at the same time, and on the other, the successive parts of a single lineage. Had these two authors used qualifying adjectives to distinguish their usages, the situation would have been far less open to criticism.

Even so, whether "the two concepts are

found to be different aspects of a single phenomenon, the only logical name for which is superspecies," as Sylvester-Bradley claims, is not certain. While clearly retaining both his own and Mayr's definitions, he indicates the definition of the superspecies in this third, inclusive, sense by means of a diagram. He states that if a geographical superspecies comprising three species *A*, *B*, and *C*, exists and their common ancestor *X* is known, then if *X* is no more different from *A* than *A* is from *B* (and presumably *C*), *X* must be included in the superspecies. His actual statement is: "*A*, *B*, *C*, and *X*, in fact, form four distinct species. *A*, however, is clearly more closely related by phylogeny to *X* than it is to *B*. Therefore, if *A* and *B* are placed in the same superspecies, *X* must also be a member of the same superspecies." This is reinforced by the legend to the figure embodying the argument, in which the whole complex (*X*, its three geographical subspecies, and the species *A*, *B*, and *C* which have arisen from them but remained allopatric) is referred to a single superspecies, "the superspecies in space and time."

There appear to be two main errors in this argument.

1. The use of the term superspecies without qualification in two different senses has led to confusion; it was for exactly this reason that I objected to it originally. In Sylvester-Bradley's example, *X* can perfectly well be a member of the chronological superspecies *X* . . . *A*, and of the chronological superspecies *X* . . . *B*, but by his own definition that cannot mean that *A* and *B* are members of the same chronological superspecies because they are not parts of the same lineage. But if by "the same superspecies" in the passage quoted above is meant the same geographical superspecies, then *X* cannot be in the same one as *A* and *B* by Mayr's definition. The argument makes sense with the definitions only if the first use of the phrase "the same superspecies" refers to the geographical and the second to the chronological meaning. Unfortunately it then becomes invalid.

2. It is not correct to say that because *A* is phylogenetically more closely related to *X* than to *B*, therefore if *A* and *B* are in the same geographical superspecies, *X* must be included as well. Sylvester-Bradley has confused here the concept of the superspecies, on both his own and Mayr's definition, with the concept of the natural group as such—a species group, genus, family, etc., according to the degree of diversity among the forms concerned. Mayr's definitions of the superspecies contain no reference to degree of close relationship phylogenetically (beyond monophylety) nor should they (Cain, 1954*b*). He states only that the superspecies consists of "a monophyletic group of geographically representative (allopatric) species which are morphologically too distinct to be included in one species" (Mayr, 1942). The basic concept is that an original population has invaded (not necessarily simultaneously) a number of ecologically suitable areas, in which some at least of the daughter populations have differentiated in isolation so far that—having regard to the sort of difference usually seen between good sympatric species in the group concerned (Cain, 1953; 1954*a*)—they must be given specific status. The resulting geographical array (*Kreis*) at any one time is what Mayr has defined as the superspecies (*Artenkreis*). If two very closely related forms in a superspecies later come to overlap widely, one of them must be excluded from the superspecies, even though it may be highly probable that both are far closer to the common ancestor than any of the other forms, which have diverged further. What Sylvester-Bradley's diagram shows is not the superspecies (in the singular) in space and time, but a monophyletic group composed to date of three allopatric radiating lineages or gentes, a time-section through which at any period, after they have diverged sufficiently to make

(Concluded on p. 139)

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.